

Foot Pressure Variability
and
Locomotor Plasticity
in Hominins

Thesis submitted in accordance with the
requirements of the University of Liverpool for the
degree of Doctor of Philosophy

by
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"To see what is in front of one's nose needs a constant struggle"

George Orwell

1. Dedication

For science,

And in loving memory of

Russell Savage

whose legacy survives in this work.

2. Acknowledgements

I am eternally indebted to my parents for their unwavering support and deafening cheers from the sideline as I've made steps to achieve this goal. Their own outstanding achievements in life have provided the direction for my own, and they are individually, and combined, two of the best role models I could wish for. This thesis also rests on the shoulders of my sister, brothers, nieces, nephews and cousins, and I am so thankful for all the different types of support and love provided by them during my university career. My family has been the bedrock from which this contribution to science has grown. To my love, Johnny Bray, there aren't words that serve to express the gratitude I have for your strong, and gentle self throughout this process. I thank the universe every day, for leading me to you. Thank you for the deep and resolute love you give me, the positive encouragement, emotional and practical support – at any time of the day or night, and the great patience and understanding you've shown toward me during this time. I couldn't wish for a better partner in crime to stand beside me through life's challenges, and to lean against when they get tough.

This work is collaborative in every sense, and my sincerest thanks are extended to the people who helped me develop it, and, the tools of science that allowed me to complete it. Any inconsistencies or mistakes presented here are surely, of my own doing. My greatest thanks go to my

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3. Co-author contributions

Chapters 17-20 of this thesis have been published, submitted or re-submitted for publication in peer-reviewed scientific journals in collaboration with four other scientific researchers: Prof. Robin Crompton (RHC), Dr. Karl Bates (KTB), Russell Savage (RS), and Prof. Todd Pataky (TCP). This thesis is presented in accordance with the guidelines of submission in the Faculty of Life Sciences, University of Liverpool, in that each paper should be integrated into the thesis in a coherent and structured manner.

This thesis begins with a general introduction and background to methods, followed by four results chapters. An overall discussion and conclusions of the thesis follows the final chapter. Supplementary materials follow the overall discussion chapter at the very end of the thesis.

Chapter 17 was published first in the *Royal Society Open Science* journal in June 2016 (McClymont et al. 2016). The concept and methodology of this experiment was developed by the author and final author KTB. KTB and RS provided initial training in the experimental equipment, and software used to analyse the experimental data, while TP provided training and analysis guidance in pSPM software. Each author provided methodological, theoretical and writing guidance to produce the

manuscript that make up each chapter. Chapter 18 developed naturally on from that preceding it. The idea and concept were developed by the author and KTB, and revision of comments for re-submission before December 2017 (McClymont et al. *in revision, a*). Chapter 19 is in the process of completing first round reviews to *Scientific Reports* (McClymont et al. *in revision, b*) in collaboration with the same four authors. The idea for the experiment was conceived by RS and KTB and the author, and training in the software for analysis was provided. All four authors provided varying levels of academic and technical support throughout the development of this manuscript, and has completed one round of external review. The concepts presented in chapter 20 were developed by the author and RHC and has been submitted for peer-review to the *Journal of Anatomy* (McClymont and Crompton, *submitted*). Following peer review, the chapter was split into two. The variability framework is *in revision* for resubmission to *Journal of Anatomy*, and the footprints analysis is *in prep* for submission to PlosONE. The fossil footprint dataset was a pre-existing registered dataset combined from Crompton et al. (2012). Training and assistance with the comparative analysis for this chapter and the re-contextualisation to examine variability in depth and pressure was provided by KTB.

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5. Ethics

All procedures were approved by the University of Liverpool Research Ethics Committee: RETH 000088.

6. Conflicts of interest

The author reports no competing interests.

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11. Definitions

Balance:

The control of movement without acceleration i.e., equilibrium.

Stability:

The biological system's ability to resist perturbations.

Stability measures:

Calculators that quantify the instantaneous motor response outputs to perturbations.

Variability:

Fluctuations in the output of movement signals e.g., stride length.

Variability measures:

Calculators that quantify the range of variability in stride time, e.g., variability in stride length can be calculated by the coefficient of variation.

Attractors:

The stable behavioural steady states of systems.

Inter-variability:

Occurring between individuals or populations.

Intra-variability:

Occurring within the individual, between strides or within steps.

Cheiridia:

Hands and feet

P-image:

A pressure record of one foot step.

Vector:

A quantity that has both direction and magnitude, determining the position of one point in space relative to another.

Locomotor mode:

A collection of actions pertaining to the movement of an animal i.e., the type of behaviour e.g., walking, brachiating, knuckle walking etc.

Stride time:

The gait cycle duration defined as the time between first contact and last contact of two consecutive footsteps.

Stride frequency:

The time between two consecutive kinematic events e.g., the time between the consecutive heel strikes of the same foot.

Stride length:

The distance between two consecutive placements of the same foot, i.e., the distance between the point the hallux leaves the ground, and the point where the heel strikes the ground in the next step of the same foot.

Constraints:

Genetic, task and environmental restrictions that act directly or indirectly on the organism during locomotion.

Torque converter mechanism:

A fluid coupling that transfers rotational force, such as that applied along the tibia during walking, to a rotating load e.g., the subtalar joint, with the

ability to multiply torque when there are differences in the input and output of rotational speed.

The windlass mechanism:

In late stance during dorsiflexion of the hallux the plantar fascia wraps around the distal metatarsal heads, shortening the distance between the calcaneus and the proximal metatarsals and lifting the medial longitudinal arch.

Chimpanzee model:

The traditional living analogous primate (*Pan troglodytes*) by which fossil locomotor interpretations were made due to the similarity in DNA. It has since been shown that Chimpanzees are derived for knuckle walking, and that *Gorilla* and *Pan paniscus* are better models by which to anchor fossil locomotor interpretations.

Anti-gravity muscles:

The extensor muscles of the knees, hips and back whose specific function is to resist the pull of gravity to maintain upright bipedal posture.

Stiffness:

Stiffness is represented by the slope of the force-displacement curve whereby the higher the slope, the stiffer the material.

Compliance:

Muscular compliance: an intrinsic property of muscle in which tension increases during lengthening without a change in neuromuscular control.

Sedimentological compliance: refers specifically to the moisture content effecting displacement of sediments by a foot step.

12. Abbreviations and units

Pedobarographic statistical parametric mapping:	pSPM
Pedobarographic record:	p-image
Zebris FDM-THM pressure sensor area:	0.717cm ²
Newtons:	N
Alpha:	α
Force:	F
Time:	t
Area:	a
Pressure:	p
Pascals:	Pa
Meters per second:	m/s
Mass:	kgs
Body Mass Index:	BMI
One dimensional:	1D
Two dimensional:	2D
Three dimensional:	3D
Centre of mass:	CoM
Centre of pressure:	CoP
Vertical ground reaction force:	vGRF
Electromyogram:	EMG
Standard deviation:	SD
Coefficient of variation:	CV

Mean square error:	MSE
Probability value:	p-value
Sample size:	n
Correlation coefficient:	r
Coefficient of determination:	r^2
Reduced squares major axis regression:	RMA
The maximum Lyapunov exponent:	λ
The maximum Floquet multipliers:	mFM
Metatarsal(s):	MT(s)
Metatarsal head(s):	MTH(s)
Metatarsal phalangeal joint(s):	MTPJ(s)
Plantar aponeurosis:	PA
Extended evolutionary synthesis:	EES
Million years ago:	MA
Thousand years ago:	KA
Stride Interval:	SI
Stride time:	ST
Pan:	<i>P.</i>
Gorilla:	<i>G.</i>
Australopithecus:	<i>A.</i>
Homo:	<i>H.</i>
Homo floresiensis foot:	<i>LB 1</i>

13. Thesis Abstract

A vast array of derived terrestrial locomotor behaviours represents multiple subspecies of primate, ranging from more arboreal vertical climbers and leapers, brachiators, and flyers, to more terrestrial quadrupedal knuckle-walkers, and obligate striding bipeds, both of whom practice occasional tripedal cantering. During terrestrial locomotor modes, the feet are in contact with the ground to varying degrees with each step, producing unique plantar pressure records with some overlap in the standard deviations of peak pressure between species. The unique pattern, generally reflects the mechanical differences that distinguish derived behaviours, such as the foot strike pattern and the distribution of peak pressure at initial foot strike. However, overlap in the distribution and magnitude of peak pressure is still clear. Similarities, or overlap in the distribution and magnitude of peak pressure, implies an underlying likeness in foot function. It is therefore surprising that a study of the variance in peak pressure in healthy humans, has not yet been investigated, or interpreted biomechanically. Here, a multi-analysis assessment of the magnitude and distribution of the variance in peak plantar pressure in healthy humans was assessed using pSPM, to establish the habitual nature of the variability. The results are presented and then used as a proxy to indicate selective pressure for locomotor plasticity in the hominin clade, through an analysis of fossil footprint trails spanning 3.66MY.

16 subjects walked for 5 minutes at 5 speeds, used consistently and without strain by healthy young adults (<65) during a normal day, producing a total sample size of between $n = 2,500-3,100$ pressure images per subject. Initial results confirmed that when calculated by mean square error, peak pressure does not follow the traditionally observed U-shaped curve that other gait parameters follow with speed. Areas of high variance are confined almost exclusively in the forefoot under metatarsal heads 5 and 1, in all subjects, and when calculated by the coefficient of variation, percentage variability is universally low (2.5%). An analysis of the sensitivity of the MSE to random sample size effects confirms an exponential increase in the total variance of peak pressure as sample size decreases. Random subsampling showed that the range in MSE only came within 5% of the overall sample size in subsamples >400, concluding that smaller sample sizes inflate the observed overall range in MSE found in a larger sample sizes (>400). Topological analysis of the relationship between speed and variance in peak pressure, confirms that changes in pressure with speed only reach statistical significance when the most disparate speeds are compared, supporting previous results. The small incremental increases in speed and the effect of the treadmill likely influence the low overall variability, and fewer statistically significant differences in peak pressure at similar speeds (1.1-1.3ms). The relationship between peak pressure magnitude with walking speed is characteristic of medial column force transfer in humans, progressing from the hind-foot to the hallux, however this general trend is

fundamentally characterised by highly variable, relative contributions of soft and hard tissues both within and between individuals in this sample. A comparative pixel level analysis of modern and fossilised footprints did not produce any meaningful statistically significant differences in the pattern of footprint depth or topology across 3.66MA, that are not accounted for by substrate effects. That there is high and low variability in peak plantar pressure in this small sample of modern humans, and, between footprints spanning 3.66MA when depth is used as analogously for peak plantar pressure, suggests the arch complex of the hominin foot is controlled by motor strategies adapted for locomotor plasticity within the hominin clade.

14. Introduction

14.1 Locomotor aptitude in humans

Human bipedal walking is characterised by an extended posture at the hip and knee, and consists of two alternating phases, swing and stance. This cyclic motion is the product of the exchange of kinetic and potential energies produced by the neuromuscular control system as it attempts to maintain stability. In each step, energy is exchanged, converted and conserved to generate the momentum required to execute the next step (Alexander, 1991, 2003; Wang, et al., 2003a,b).

The foot alternates periods in contact with the ground when it is both stable and propulsive, termed stance phase, and a forward swinging period in which the foot prepares for the next ground contact, termed swing phase. It is widely thought that the human foot is specialised and unique amongst apes for efficient, upright locomotion (Lewis, 1980; Ker, et al., 1987), specifically the derived Achilles tendon, plantar aponeurosis (PA) and medial, longitudinal and transverse arch complexes (Aiello and Dean, 1990; Harcourt-Smith and Aiello, 2004). As humans are most closely genetically related to the chimpanzees (*Pan spp.*) (Friday, 1992; Goodman, 1992; Sibley, 1992); and as *Pan troglodytes* (*P. troglodytes*) was the first chimpanzee to be studied intensively (Goodall, 1972), it was traditionally accepted as a suitable locomotor analogy for early hominin origins

(Jenkins, 1972; Bauer, 1977; Alexander and Maloiy, 1984); Chimpanzee locomotor behaviour however is derived, with matching inertial properties between the fore- and hindlimb (Isler, et al., 2006; Myatt, et al., 2011, 2012) and metacarpal length (Drapeau and Ward 2007) facilitating effective, pronograde quadrupedalism. Functional and locomotor similarities supported by morphological overlap do, however exist more prominently in the ratio of human and *Gorilla* cheiridia (Schultz, 1927, 1930). Venkataraman et al. (2013a,b) also reported overlap in distal tibial morphology in modern human arboreal foragers, as adequate to counter derived features of the ankle associated with bipedalism. The great capacity for functional movement in the *Homo sapiens* foot is in part made feasible because of the anatomical complexity of the structure.

14.2 The anatomy of the foot

The human foot is a lattice of 24 bones, and over 100 muscles, ligaments and tendons (Figure 1a-g) making it a highly complex and adaptive structure (Crompton, et al., 2008). It is generally thought that the foot is specialised in possessing a rigid, low, lateral longitudinal arch, and a compliant, high medial longitudinal arch (Aiello & Dean, 1990) (Figure 1h-j). These structures lie at a right angle to the Achilles' tendon and extend horizontally from the heel, combining with the plantar aponeurosis (PA) that extends longitudinally along much of the length of the plantar surface. Combined, they act as springs to control the exchange of elastic and strain energy during stance (Caravaggi, et al., 2010). The

first contact between the foot and the ground is under the heel (heel-strike), then contact propagates along the lateral arch as far as the middle of the metatarsals (MT) (mid-stance), and thence proceeds medially to the metatarsal heads (MTHs) toward the base of the hallux (toe-off) (De Cock, et al., 2007, Figure 1k-m). This action works to lever the centre of mass (CoM) over the base of support and in humans, is ordinarily considered stiffer than the feet of other living primates, to support upright, striding and terrestrial gait. In contrast, it is held that non-human apes practice a range of quadrupedal and bipedal behaviour, demonstrating grasping behaviour with their feet typically via flexion at the midfoot. During stance phase, first contact is under the midfoot then propagating forward a the lateral MTs, thus propulsive force is exerted from the midfoot rather than the toes (Harcourt-Smith and Aiello 2004).

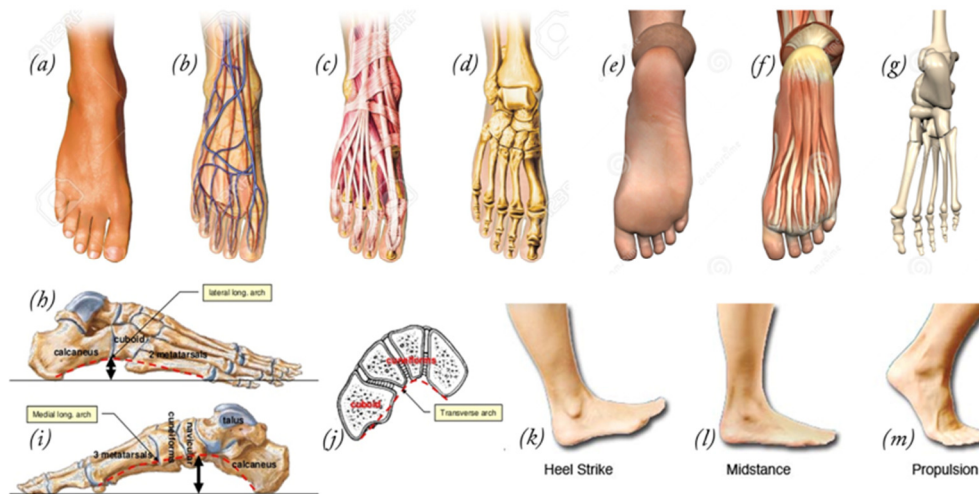


Figure 1

Cutaway representations of the gross and superficial bones and muscles of the human foot from dorsal (a-d) and plantar aspects (e-g). The longitudinal and transverse arches are indicated by red dotted lines (h-i): the lateral longitudinal arch is comprised of the calcaneus, cuboid and MTs 4 and 5 (h). The medial longitudinal arch is comprised of the calcaneus, talus, navicular and 3 cuneiform bones and MTs 3-1 (i). The transverse arch is formed by the cuneiform, cuboid and the proximal bases of the MT complex (j). Stance phase is characterised by three functional time phases: initial heel strike where declarative forces are applied and absorbed through the calcaneus (k), midstance where by the midfoot is in contact with the ground absorbing and transferring force along the MT diaphyses (l), and toe-off through which the body gains maximum propulsive forces to and from the ground, driving the leg into swing phase (m). Image credits; a-g: www.alamy.com/DCG48B, h-i: www.slideshare.net/Dr.AkramJaffa, k-m: drschnowske.blogspot.com.

14.3 The centre of pressure

The interaction between the foot and the ground is illustrated by the path of the centre of pressure (CoP), classically described as the instantaneous point location of the vertical ground reaction force (vGRF) vector experienced by the plantar surface against the ground (Winter and Yack 1987; De Cock, et al., 2007, Figure 2a). During mid-stance, the CoP shifts medially approximately from the mid-distal-diaphysis of the MT complex, moving across the dorsiflexing MTHs (Close, et al., 1967, Figure 2a). During toe-off, the CoP lies distal to the MTHs, exerting maximum propulsive power from the hallux (in shod Western modern humans), second and/or third phalanx (in habitually unshod modern humans) (Figure 2b) (D'Août, et al., 2009; Rolian, et al., 2009; Crompton, et al., 2010). In more detail: from heel strike, the CoP travels along the lateral longitudinal arch (Ker, et al., 1987) via the components of the torque-converter mechanism (Figure 2c) (Wolf, et al., 2004). This mechanism translates axial rotatory forces joint-by-joint from the hip, through the knee, to the subtalar joint and finally to the forefoot. At this point, axial rotation is converted at the subtalar joint into tri-planar rotation in the frontal plane from the talus to the more distal tarsals and along the MT's,, initiating the common medial roll-over pattern forming the path of the CoP against the ground (Figure 2b,c) (Hestenes, 1999; Wolf, et al., 2004,).

The torque converter mechanism driving the lower leg, is reflected in human plantar pressure records (p-images) by three highly variable

functional units defined by increasing and decreasing pressure: a passive ground-impactor (high pressure at the heel), a secondary absorbent and propulsive lever that responds to changes in muscular stiffening (decreasing pressure in the midfoot and proximal forefoot), and a propulsion mechanism to complete stance phase (increasing pressure in the forefoot and phalanges to toe-off). Variation in, and discrete metrics of pressure including the CoP and the vGRF from p-images, are used widely to diagnose and evaluate foot abnormalities (Frykberg, et al., 1998; Pham, et al., 2000; Boulton, et al., 2004); identify potential medical interventions (Bus, et al., 2008; Paton, et al., 2011); provide insights into the modulation of foot function during a range of activities (Pataky, et al., 2008); and compare differences in foot function across time in the primate clade (Vereecke, et al., 2003; Crompton, et al., 2012).

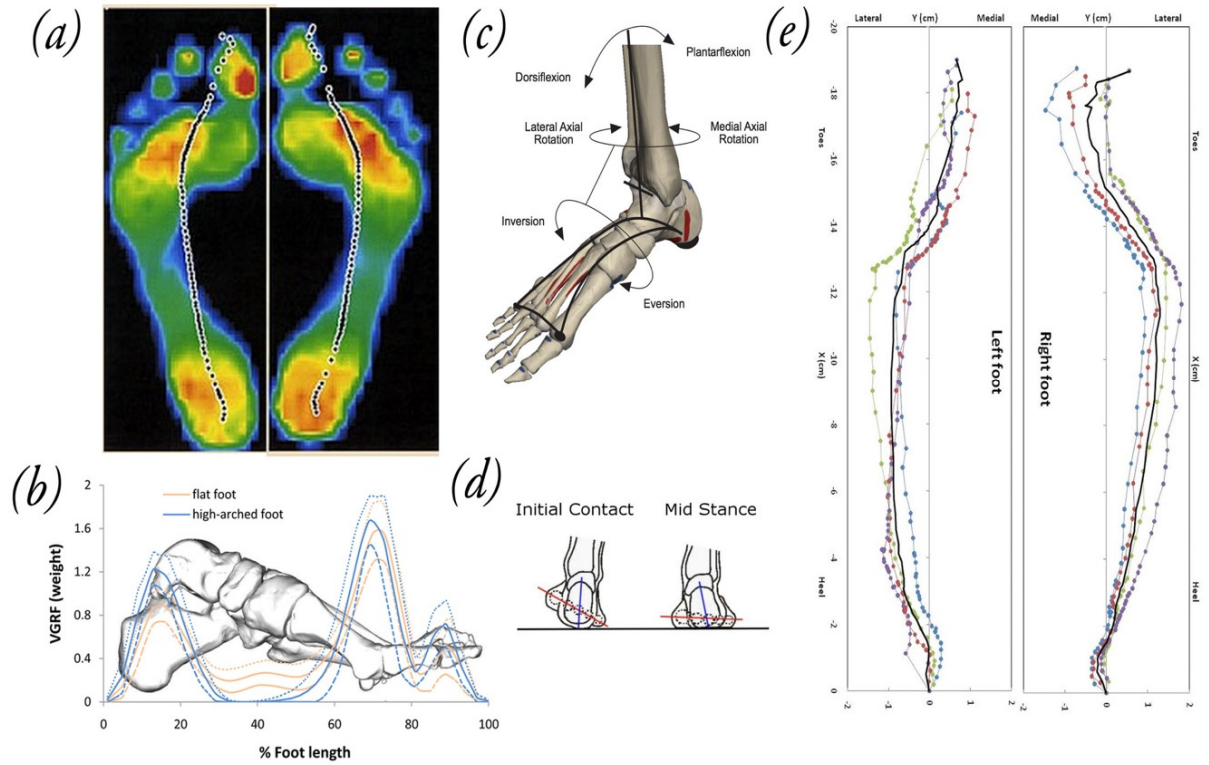


Figure 2

The path of the CoP, i.e., the point location of the vGRF vector applied to the plantar surface of the foot when in contact with the ground (a) is highly variable depending on individual morphology (b). During walking, the torque converter mechanism accelerates the translation and conversion of axial rotation from the knee, into frontal tri-planar rotation (inversion/eversion) at the foot (c), producing the characteristic medial rollover trajectory during stance phase humans (d). The estimated path of the CoP shows high spatial scatter particularly at heel strike and toe off in healthy adults because of low pressures exerted on the force plate during these phases (e). Image credits: a: reprinted with permission by Robin Crompton, b: Fan et al. 2011; c-d: skimovesme.com).

14.4 Non-human ape plantar pressure

P-images are perhaps the best available proxy for interpreting internal loading patterns of the foot (Stéphane, et al., 2008), particularly when combined with external foot bone kinematics (Bates, et al., 2013a; Caravaggi et al. 2016). This proxy is supported by recent modelling results that revealed a direct causal relationship between internal foot motion and the pattern expressed as plantar pressure (Caravaggi, et al., 2016).

The path of the CoP is a product of the neural control mechanism of the ankle (Winter, 1995). The ankle experiences increasing plantarflexion during stance phase drawing the CoP anteriorly, while consequentially, inverter activity initially moves the CoP laterally (Winter, 1995) before shifting medially. In contrast, some non-human apes (*Gorilla*, *Hylobates*, *P. troglodytes* and *Pan paniscus*) tend to bear initial touch down at the mid-MT diaphyses experiencing almost simultaneous hindfoot and midfoot touchdown (Figure 3c-f). The CoP then propagates forward from the midfoot to the lateral phalanges from where maximum propulsive force is exerted (Wunderlich, 1999; Vereecke, et al., 2003). Orang-utans however, often produce a heel-strike (Crompton, et al., 2003). Plantar pressure studies identified peak pressure under MTH1 and 3 during quadrupedal locomotion and under MT2 and 3 followed by MT1 and 4 in pole climbing, subjecting MT1-3 to the highest peak plantar pressures most frequently. The differences in patterns between primates are a product of the frequency by which unique locomotor modes are practiced (Figure 3a-f),

producing unique and derived morphology and mechanics i.e., the torque converter and roll-over mechanisms. While these differences are unique, the standard deviations (SD) of peak pressure overlap between humans, *Gorilla*, *Pongo*, and *P. paniscus* are evident (Vereecke, et al., 2008; Crompton, et al., 2010) suggesting an underlying broad similarity.

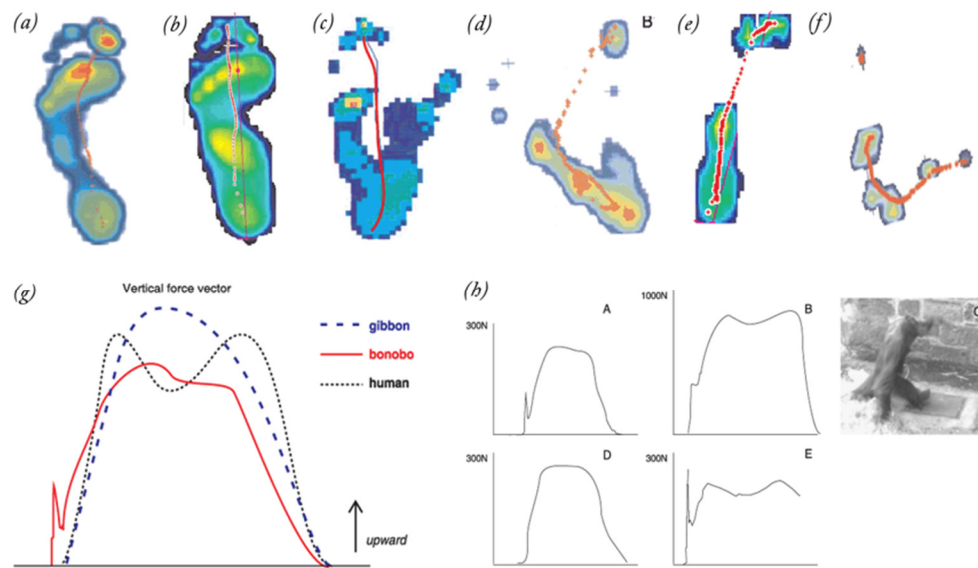


Figure 3

The general path of the CoP in living primates: Western modern humans (a,b), gorillas (c), bonobos (d), orang-utans (e), and gibbons (f) showing the variability in CoP trajectory in these primates. Subject (b) is an example of a modern human with a lateral midtarsal break expressing a slightly more medial trajectory relative to (a). This trajectory is within the range of human variation. Image credits: a-f: collected and reproduced by the EMBRG and reprinted with permission; g-h: Crompton et al. 2007

14.5 Human foot evolution

The study of locomotor performance in humans, as in all biological systems, represents an important link between phenotype and ecological and reproductive success and thus, predicting locomotor behaviour from hominoid fossils is a focus for understanding the evolutionary adaptation of movement in humans (Koehl, 1996; Alexander, 2003). Our present understanding of the evolution of foot function from bipedal walking is based on interpretations of the fossil record of hominins.

Traditionally, movement interpretations from fossils were founded in a theoretical framework grounded in the reductionalist or ‘medical’ model (or the Platonic ‘ideal’), whereby differences in morphology reflects differences in locomotor modes. Differences in pressure amongst some primates were distinguished from pressure images interpreted in a classic study by Elftman and Manter (1934, 1935), which hypothesised that humans differ from other apes in lacking a so-called ‘midtarsal break’, where the lateral midfoot first contacts the ground exposing a pressure peak in this position. This hypothesis was elaborated on further by Böjsen-Möller (1979) who attributed the lack of a midtarsal break in humans to the projection of a peg from the plantar aspect of the cuboid, which interlocked with a matching groove on the plantar calcaneus, predicted to effectively lock the midfoot, causing a stiff midfoot.. Around the same time in the medical sciences, the Root model (1975) was developed, defining three modal conditions of the human foot, *pes planus*,

pes normalis, and *pes cavus*, describing deviations from *pes normalis* as dysfunctional. Following this model, Jungers, et al., (2009) for example, note limited prominence of the cuboid peg in LB 2 (*Homo floresiensis*) fossil foot, concluding that this species must have differed from *H. sapiens* in function of the lateral longitudinal arch. As is evident in Figure 3b, humans can also express a non-pathological midtarsal break. This is discussed with further examples in chapter 18.

More recent locomotor interpretations from fossil remains reject the Root model, due to the reported relatively high occurrences of midtarsal breaks (Bates, et al., 2013b; DeSilva and Gill, 2013) and high inter-tarsal joint motion observed in modern humans (Lundgren, et al., 2008; Nester, et al., 2007a,b). Furthermore, human peak pressure values have been reported to overlap with orang-utans and bonobos (Crompton, et al., 2010; Vereecke, et al., 2008). Recent interpretations of hominin fossils also embrace the idea that hominins probably exploited a variable locomotor spectrum adaptable to variable environments (Zipfel, et al., 2010; DeSilva, et al., 2013). The current consensus generally expresses that hominins could in fact exploit various modes of locomotion, thanks to the “mosaic” expression of morphological traits found overlapping between species. While the idea of locomotor plasticity is generally discussed in the literature, there remains to be presented a theoretical paradigm by which to explain, compare and contrast the observed variability in morphological traits that facilitates such vast locomotor

abilities. It can be argued that analysis of bone shape in isolation does not definitively test behaviour or locomotor mode, as relative contributions of soft tissues, relationships between applied forces, and the moving dynamics of the system are not accounted for. Given the truly fragmentary nature of the fossil record, it is not uncommon that an *n* of one skeletal element is available to characterise taxa and locomotor behaviour; and more often than not, the variability and overlap in bone shape, as in peak pressure, is cited but regularly not elaborated on. It is not suggested here that the limitations associated with comparative functional morphology and small sample sizes reduce the interpretive strength of pre-existing locomotor predictions. However, this thesis suggests that biomechanical and morphological interpretations of fossil bones could be embedded within a strong interpretive framework that explains variability within the constructs of the inherent movement abilities of biological systems.

14.6 Dynamical systems theory

At a similar time to Elftman and Manter's (1934, 1935) studies a different paradigm was being developed by Nikolai Bernstein to interpret human movement, under the existing interpretive framework of dynamical systems theory (Bernstein, 1967). The principles presented attempted to explain coordination and movement, being adapted from the broader principles of chaos theory, primarily able to interpret long-term qualitative change in the behaviour of dynamical systems. Dynamical systems theory has emerged in the movement (Glazier, et al., 2003;

Handford et al. 2007) and cognitive sciences (Beer, et al., 2000; Schöner, 2008) as a viable framework for interpreting adaptive behaviour in human biomechanical systems by quantification of the variability and stability inherent in biological systems (Newell, 1986; Handford, et al., 1997; Davids, et al., 2003; van Emmerik, et al., 2016).

Bernstein's application of dynamical systems theory to biomechanics considered (amongst other things), how abundant degrees of freedom in complex systems produce locomotion, specifically how independent variables in a biomechanical complex are regulated with minimal energetic cost to produce smooth movements. By incorporating aspects of non-linear dynamics in human movement studies, he suggested that much of what would appear to be non-functional noise, reflected the ordering of chaotic, deterministic processes defining movement (Bernstein, 1967). Later developments in coordination and motor learning built on Bernstein's ideas to reveal collective 'self-organisation' and coordinative neuro patterning of deterministic processes. These were discovered to regulate movement in systems characterised by high levels of coexisting and independent structures (Turvey, 1990). The 'order from chaos' described here, also underlies the phylogenetic nature of variability in biological systems (Bock, 1965; 1994), and as such the relative influence of genetics and the environment are important for the interpretation of locomotion in hominin evolution. A short discussion on how biological systems interact with an environment is presented here.

Self-organising patterns in locomotor strategies emerge from interactions between 'organisation states' that change relative to internal and environmental constraints, pressuring the system into adaptive states (Kugler & Turvey, 1987). The morphology of bones is largely dependent on the movement practiced by the individual during life (Bock, 1965; Gould & Lewontin, 1979) and is a fundamental interpretive tool in bioarchaeology and palaeoanthropology in the study of fossilised skeletal remains (Jungers and Minns, 1979; Trinkaus and Ruff, 1999; MacLatchy, et al., 2000; Madar, et al., 2002; Ruff, 2002; Ruff, et al., 2006). It is widely accepted in these fields that bone functional adaptation is the product of the dynamical systems interaction with the environment (Ruff, et al., 2006). Locomotor ability and performance are often unique to sub-species; thus, successful locomotor behaviour will naturally increase the reproductive success of the individual. The differential reproductive success of many individuals within a population is the central premise of natural selection. Just as individual performances are responsive to individual constraints e.g., injury and the environment, locomotor performance is responsive to inherited morphological constraints and the environment at a population level.

14.7 Motor control of movement

Thus, locomotor performance is highly complex and adaptive (Newell, 1986; Latash, 2000), producing highly diverse locomotor modes amongst primates (D'Août, et al., 2004) and hominins (Zipfel, et al., 2011; Crompton, 2015). In part, this is due to the variable phylogenetic and environmental history within which the locomotor system evolved, but is also due to a set of defining physical principles driving the movement of complex biological systems (Shannon and Weaver, 1949). These include the individual process by which chaotic systems are ordered to produce functional movement. Walking is regulated by interactions between the neural and sensorimotor systems (Latash, 1993). The two systems continuously update, integrate and coordinate multiple sensory, and motor pattern inputs and outputs producing a continuous striding gait (Dingwell and Cusumano, 2015). Motor task patterns are unique for all tasks, and unique strategies are assembled for each step to achieve the most stable step (task) outcome (Brisson and Alain, 1996).

The step-to-step strategy is highly adaptive to account for expected or unexpected changes in the environment such as; slope and substrate compliance, and accelerations and decelerations produced from these changes, and are formally termed as constraints (Newell, 1986; Davids, et al., 2003; Latash, 2000; Davids, et al., 2003). In primates, it is the cheiridia

that interact directly with the environment and expectantly, these are two of the most anatomically complex structures in the body.

To present this differently, an integrated, complex system can be broken down into n component parts, and change in the system plotted over time, producing an n -dimensional state space (Kauffman, 1993). For example, while the foot is in contact with the ground during walking, the n components of the system can all change in value during this time, and vary with each step to a greater or lesser extent. Coordinate points of interacting components and micro-components can be quantified during a movement cycle, and can be plotted and connected to form a trajectory, e.g., a joint centre trajectory. The coordinative path of the system is entirely dependent on the internal and external constraints: environmental (e.g., change in substrate), organismic (e.g., ankle injury), task (e.g., turning) (Newell, 1986).

Biomechanical movement however is characterised by the ability to move and adapt in usually complex 3D space. The system components and micro-components coordinate and adapt to topological 3D state space by providing quick, temporary moments of stability (Kauffman, 1993; Handford, et al., 1997). When quantified by the Lyapunov exponent (λ), smooth walking style is stable, while rugged walking style is often unstable (Rosenstein, et al., 1993; Dingwell, et al., 2001), and the difference between them reflects the systems exploration of different

“attractors”, i.e., ‘temporarily assembled moments of stability established relative to system constraints’ (Latash, 2000), that enable and maintain upright stable walking.

The attractors represent the state space by which the components of the system can coordinate together to produce temporary task outcomes (Kelso and Ding, 1994). How the system shifts in and out of different attractor states is driven by ‘order parameters’, and ‘control parameters’. Order parameters are the structural organising states of the system representing coordination: e.g., the differences in relative phase in the exchange of potential and kinetic energy when switching from walking to running (Kelso, 1995). Control parameters describe the pattern organisation of the dynamic system, e.g., a change in substrate, or limb oscillation frequency (Haken and Wunderlin, 1990). A small change in an order parameter can lead to significant changes in control parameters: for example, an influx of kinetic energy into the limbs (order parameter) increases the limb oscillation frequency (control parameter) changing it from an attractor state for walking, to an attractor state for running.

Human movement is thus described as a dynamic system searching for relevant coordinated solutions in order to engage in functional activity (Handford, et al., 1997). This description allows us to consider the body as a highly complex and adaptive system that changes over time relative to internal and external constraints. When constraints change, attractors are

relocated to other parts of the body to coordinate with the new constraint. Thus, each temporary task outcome provided through the attractor state is different from the state before and after it. The combined differences in trajectories of each stable moment solution represent the distribution – or variability - of the variability or stability parameter being measured.

14.8 Quantifying variability

Bernstein described variability as “repetition without repetition”: e.g., if a ball is thrown ten times against a wall, then the trajectory of the ball, and the movement that produces that action, will be different each time. Similarly, each step during locomotion will be different, thus changes in kinematics (e.g., joint motion), and kinetic patterns (e.g., muscle firing patterns) observed during gait, account for the differences observed in people walking (Dingwell and Cusumano, 2015). Thus, one of the most common features of walking is motor variability (Latash, et al., 2002).

Movement variance is indexed by the SD, representing the distribution of the data set trajectory (Newell, 1986). While definitions of variability range across the literature, modern statistical definitions of variability express it as the variance (or, the square root of the variance, i.e., the SD) about the mean (Riley and Turvey, 2002) of the dependent variable, over repeated trials (Davids, et al., 2003). In the last thirty years, the interpretation of variability has developed from ‘non-functional noise’ (Kelso, 1995), to being considered as a defining characteristic of the

human locomotor system (Arutyunyan, et al., 1969; Newell, 1986; Latash, et al., 2002; Davids, et al., 2003). Intra-individual variability is the quantifiable difference in the motor pattern outputs, variably powering the relative movement of body segments through the exploitation of ample degrees of freedom, to produce walking movements (Newell & Corcos, 1993). There is variability in all the systems that control the multiple components of walking, such that each step is characterised by differences in time, length and width, but also in the apparent rhythmicity of contralateral limb movements, exhibited in time-variations in relative phase (Schmidt, et al., 1991). As mentioned previously, variability can increase or decrease relative to the environment, organism and task constraints (Newell, 1986). Thus, variability in kinematic or kinetic parameters is considered neither necessarily beneficial nor detrimental (Davids, et al., 2003). Studies that assess variability in kinematic and kinetic parameters with speed are common, showing that changes in variability can increase energetic costs and step parameters such as step time, length and width with changes in speed (Jordan, et al., 2007a; Grabiner, et al., 2001; Owings and Grabiner, 2003), with linear increases in the variability of joint angles (Öberg, et al., 1993), step length (Glazier, et al., 2006), step time interval (Beauchet, et al., 2005) and step impulse (Winter and Yack, 1987). Regardless of parameter the linear changes in variability commonly follow a U-shaped dependency with speeds faster and slower than comfortable walking speed (Winter and Yack, 1987; Öberg, et al., 1993; Brisswalter and Mottet, 1996; Winter, et al., 1990;

Stolwijk, et al., 2013; Carrier, et al., 1994). Thus, the coordination of such a mechanically abundant system, provides vigorous and energy efficient functional performance through high functional variability (Zarrugh, et al., 1974; Handford, et al., 1997; Davids, et al., 2002; Kuo, 2001; Braun, et al., 2009; Dingwell, et al., 2010), described as “optimum noise mixed with regularity” (Hong, et al., 2006). This is widely termed “complexity” Complexity in the motor system is generally reduced with age and illness causing a reduction in functionality due to a reduction in the ability to adapt to changes in the environment (Newell and Vaillancourt, 2001).

Changes in step variability are associated with unsteady gait (Heiderscheit, 2000) and with higher fall-risk in older people (Gabell and Nayak, 1984; Hausdorff, et al., 1997; Maki, 1997), thought to be due to a decline in proprioception and a reduction in protective reflexes due to the ageing process (Rubenstein, 2006). Adults over 65 years old tend to show higher magnitude changes in variability in frontal hip and knee motions, knee internal and external rotation, trunk motions (Kang and Dingwell, 2008) and step width (Beauchet, et al., 2007), when walking at speeds that are faster, or slower than their comfortable walking speed (Jordan, et al., 2007a; Kang and Dingwell, 2008). The underlying meaning and functional importance of variability as a causal mechanism of gait, remains unclear (Dingwell and Martin, 2006; van Emmerik, et al., 2016). Tracking variability across ontogeny is useful, in order to understand how the nervous system regulates the ageing process (Dingwell and Cusumano,

2015), and how it develops and adapts to fluctuations that occur during complex movement tasks such as walking (Todorov, 2004; Cusumano and Cesari, 2006).

15. Aims and objectives

15.1 Aims

The preceding sections attempted to convey the message that foot-ground interactions are one of the key components in understanding development and change in gait over time. In terms of dynamic systems theory, the foot-ground interaction experiences the three constraints driving adaptive locomotor behaviour, i.e., the organism (the foot), the environment (the substrate) and the task (walking) as described by Newell (Newell, 1986). However functionally determined explanations that explain the variability in magnitude and spatial distribution in plantar pressure have not been established. Currently, variation in peak pressure cannot be described as the variability itself has not yet accurately analysed or described. Regionalisation of the plantar surface, small individual trial n , and self-selected walking speeds are three potential biases affecting interpretations of peak pressure due to the complex and functional nature of the foot-ground interaction. These limitations were not factors in the experiments herein. As the only part of the human body to consistently interact with the environment, and the innate nature of variability in biological movement, a natural extension of this project is to consider the effects of variability in the evolution of the human locomotor system.

15.2 Objectives

The objectives of each chapter of this thesis are outlined here and developed subsequently within each chapter:

- 1: To determine the magnitude and spatial distribution of peak plantar pressure variability by MSE and CV equations (chapter 17).
- 2: To explore the effect of walking speed on peak pressure in datasets with a high individual trial n ($n = >500$) (chapter 18).
- 3: To quantify the average rate by which the MSE in peak pressure varies in response to random sample size effects (chapter 19).
- 4: To explore locomotor plasticity as a strong selective target for hominin locomotor evolution, contextualised on an abundance of mechanical redundancy of, and high intra-variability in motor systems, and explore the potential for more accurately interpreting hominin locomotor evolution through a variability framework (chapter 20).

16. Materials and Methods

16.1 Materials

The results presented in chapters 17-20 are generated from a large dataset collected solely by the author. A total of 16 subjects (11 males, 5 females, aged 21-47 years, Table 1, DOI: [10.5061/dryad.09q2b](https://doi.org/10.5061/dryad.09q2b)), without pathologies, abnormalities or injuries, walked barefoot on a Zebris FDM-THM plantar pressure sensing treadmill (Zebris Medical GmbH, Isny, Germany) at controlled speeds of 1.1m/s, 1.3m/s, 1.5m/s, 1.7m/s, and 1.9m/s, for 5 minutes in a randomised trial order. The slowest speed (1.1m/s) was selected as slower than a 'comfortable' walking speed for healthy cohorts 20-50 years old (Bohannon and Andrews, 2011). It is acknowledged that 'comfortable speed' is relative to different ages and abilities, however 1.1m/s may generally be considered slow for healthy young cohorts such as are the participants of these trials. The fastest speed, 1.9m/s, was chosen as the closest speed to the accepted walk/run transition, after which walking becomes economically inefficient at 2.0m/s (Margaria, 1976). None of the subjects adopted a running gait at 1.9m/s. Increasing speed in increments at 0.2m/s (1.3m/s 1.5m/s and 1.7m/s) approximately 20% was chosen for intuitive ease of analysis.

During data collection, the subjects were asked to look at a point on the wall approximately 5m ahead of them. The order of speed collection was randomised for each subject. Subjects practiced the speed for 10

seconds before data collection began, and continued to walk for 10 seconds upon completion of data collection for each speed. Subjects took a 5-minute rest between each speed trial. Data collection was triggered on the 11th step, and as a further guarantee of reliability, the first two steps collected in each trial were eliminated. Thus, the 11th step was taken as the template for registration.

Table 1

Summary anthropometric and *n p*-image data from the 16 healthy subjects participating in this study with no injuries, pathology or high BMI. Leg length, was measured as the proximodistal distance from the greater trochanter to the mid-plantar-lateral surface of the foot. Different aspects of this dataset are analysed in chapters 17-20. 'Letter coding' column represents the letter assigned to each subject throughout the analysis.

Gender	Age (Yrs)	Leglength (cm)	Height (m)	Mass (kgs)	BMI	<i>n</i> = 1.1ms	<i>n</i> = 1.3ms	<i>n</i> = 1.5ms	<i>n</i> = 1.7ms	<i>n</i> = 1.9ms	Letter coding
M	21	0.905	1.74	75	24.8	528	583	626	668	694	A
M	28	1	1.91	78.6	21.5	526	544	577	613	622	B
F	24	0.83	1.65	59	21.7	574	600	628	687	721	C
M	27	0.925	1.85	83.3	24.3	516	558	593	641	688	D
M	22	0.965	1.96	82.7	21.5	475	533	562	608	646	E
M	26	1.3	1.75	86	28.1	486	520	562	590	622	F
M	29	0.885	1.75	70	22.9	533	591	607	644	702	G
M	30	0.905	1.7	87	30.1	526	568	568	654	665	H
F	31	0.85	1.58	52.7	21.1	560	612	651	694	746	I
M	31	0.92	1.73	74	24.7	502	553	586	651	707	J
M	44	1	1.93	80	21.5	504	573	597	630	660	K
F	37	0.94	1.63	63	23.7	529	577	594	622	649	L
F	37	0.83	1.56	52.7	21.7	611	663	692	751	818	M
M	24	0.89	1.75	81	26.4	523	563	614	646	686	N
F	23	0.85	1.58	64.4	25.8	578	614	687	708	765	O
M	20	0.96	1.85	73	21.3	513	571	599	624	659	P

16.2 Methods

The method used herein is adapted from statistical parametric mapping (SPM), originally developed to assess regional blood flow in PET and fMRI images (Friston, et al., 1995; Pataky and Goulermas 2008). As in functional brain imaging, pedobarographic Statistical Parametric Mapping (pSPM) is suited to the analysis of pressure due to the biological similarities between the brain and foot: they are bounded, representing within the bounds a single, smooth, functional unit, and possess a quantifiable spatial field within its own structural boundaries. (Pataky 2012). This method and analysis reflects relative changes in pixel values that occur directly as a consequence of organ function (Friston, et al., 1995; Pataky and Goulermas, 2008). Biomechanical experimentation measures the underlying forces that produce movement, from joint centres or from the path of physical bodies through space. They are often represented by one-dimensional (1D) scalar trajectories ($y_1(q)$), defining the direction of the joint or axis (i), through 1D time and space (q) (Pataky et al. 2013). Typically, the variables are exposed to repeated measures and a registration process (Sadeghi et al. 2003). However, the variable nature of biomechanical data and hypothesis testing exposes it to many potential sources of bias (James and Bates 1997; Knudson 2009; Pataky et al. 2013), including directed and non-directed null hypothesis testing that have the potential to cause both post hoc regional focus bias, or inter-component covariance bias (James and Bates 1997; Knudson 2009; Pataky et al. 2013). Furthermore, traditional analyses of plantar pressure are linear,

applied to regionalised units of the plantar surface. This method however relies on an independence between regions, and has been shown to conflate statistical analyses particularly along regional borders when compared to a topological field approach. pSPM alleviates potential source bias and treats the plantar surface as a singular functional unit, mitigating the need for regionalisation. The data:

$$(y_i(q))$$

is regarded as a continuous vector field $\mathbf{y}(q)$ comprised of multiple component vectors (\mathbf{y}) that change in direction, time and space relative to movement in (i) (Friston et al. 2007). Additionally, random field theory calculates the probability that changes in the vector fields are a product of fluctuations in chance vector fields (Alder and Taylor, 2007; Pataky et al. 2013).

pSPM registers datasets of p-images pixel by pixel in a two-way translation and transformation process, so that homologous structures overlap. Repeated registration combines individual speed trial datasets from each subject of the 5 speed trials. Here, when comparing speed trials e.g., 1.1 to 1.9m/s, a t-statistic (an analysis of the difference between the two pixels) is applied. If the t-statistic of one pixel is larger than $\alpha = 0.05$, then it is statistically significant, e.g., one pixel is significantly different from the other. The underlying statistical comparison relies on the fact that each parametric statistical test conducted at the pixel level is

continuous with known topological characteristics.

One problem however, is that a lot of t-tests are being conducted across the surface, $\alpha = 0.05$, assuming 5% of the pixels in the field will be expected to have p-values lower than 0.05, simply by chance. Because there are a lot of t-stats being conducted, the risk of a type 1 error increases, thus a Bonferroni correction is applied. Bonferroni correction compensates for the potential of producing error by conducting each test at α/n t-tests. Each hypothesis is thus tested in this way.

Finally, reduced major axis regression was applied to both topological and non-topological analyses to assess the correlation between two independent variables, (pressure and walking speed) with independent error possible (likely) in both measurements. Topological RMA by pSPM is an appropriate choice for analyses of plantar pressure due to its analysis of the symmetry of the relationship between the two variables, i.e., the underlying relationship calculated, represents the estimated relationship between the dependent and independent variables, as they are asymmetrical. That is: pressure increases or decreases (y) with speed (x) variably, across the whole pressure field. The geometric mean functional regression relationship produces a unique estimated slope of the variables regardless of whether x regresses on y , or y regresses on x , and is thus, symmetrical. The relationship between pressure and walking speed by RMA represented herein, represent the geometric, mean functional relationship between pressure and walking speed from the

whole pressure field. Specifically, the increasing and decreasing pressure represents the difference between the regression slopes of the two variables. The advantage of RMA regression is that it exposes the inconsistencies in the data sets and accounts for noise and error by minimizing the area of the triangle between the pressure value and the slope.

The dataset analysed herein was collected on a Zebris FDM-THM plantar pressure sensing treadmill (see above) to capture a reliably representative sample i.e., high individual trial n of plantar pressure records by which to interpret variability in accordance with the biomechanics literature (Dingwell, et al., 2001; Owings and Grabiner, 2003; Hollman, et al., 2010; van Schooten, et al., 2012; Riva, et al., 2013).

An underlying force plate embedded in the treadmill, captures global force vectors from each cell loaded by the foot producing p-images that represent the plantar surface as a whole pressure field. Each pressure cell (0.717cm^2) contacted by the foot captures the force value applied to it, producing smooth and bounded (by foot shape) p-images. The p-images within are comprised of two important mathematical characteristics found in all biomechanical data: [i] it is spatiotemporally smooth, due to the viscoelastic properties of soft tissue (Fung, 1981), and [ii] is distributed step-to-step within consistently shaped boundaries e.g., biological i.e., foot shape, or temporal i.e., step time. These features permit

the registration of large datasets allowing continuous comparisons of multiple field observations, and robust The nature of the brain and the foot facilitate statistical correlations between local data (Maintz and Viergever, 1998; Pataky, 2010). Here the ‘field’ refers to the continuous pressure pattern defined by pixel values bounded by the shape of the foot, i.e., a p-image. One limitation when comparing prints through the translation and registration is that slight differences in contact area in each step cause pixels to appear significant around the edges of the print. This could be removed with a more flexible algorithm or – non-ridged body image registration approach. This technique works to optimise image similarity with respect to the transformation parameters defined by the registration code. A more flexible algorithm would consider the variability in contact area step-to-step. This approach is not applied herein due to the lack of functionally significant movement around the edges of the p-images, where differences in contact area occur most often.

Such advances in techniques have aided departure from the reductionalist approach applied to the analysis of mean and peak pressure datasets, however ‘anatomical masking’, or ‘regionalisation’ of the plantar surface is still used widely (Hughes, et al., 1991; Rosenbaum, et al., 1994; Zhu, et al., 1995; Kernozek, et al., 1996; Brown and Mueller, 1998; Drerup, et al., 2001; Burnfield, et al., 2004; Segal, et al., 2004; Taylor, et al., 2004; Warren, et al., 2004; Yang, et al., 2005; Shu, et al., 2010; Paton, et al., 2011; Barn, et al., 2015; Howcroft, et al., 2016). A comparison of pSPM and

anatomical masking techniques revealed conflation of values at regional boundaries using a regionalised approach (Pataky, et al., 2008). Comparatively pSPM is highly generalised and flexible, providing statistically significant inferences that represent entire functioning fields, and the underlying biological meaning (Friston, et al., 1995; Pataky and Goulermas, 2008) and has been validated widely (Worsley, et al., 1992, 1995, 1999).

pSPM spatially assess the relationship of the vector values between neighbouring pixels (0.717cm^2) of p-images capturing absolute pressure values and converting their distribution to represent a topological surface (Friston, et al., 1995; Pataky and Goulermas, 2008). From the topological surface, a customised algorithm transforms, thresholds, and registers each p-image to each other, minimising the error between pixels so that optimal structures overlap (Pataky and Goulermas, 2008).

Herein, the variability in pressure is calculated by the mean square error (MSE) (chapters 17, 18, 19) and the coefficient of variation (CV) (chapter 17). The MSE reflects the absolute variation in pressure values from each pixel in the p-image, minimising the natural error that occurs between pixel vector values (Pataky and Goulermas, 2008). MSE is not the most commonly chosen calculator for variability in biomechanical analyses, but has been successful in calculating mean value characteristics, and inter-day reliability of the vertical ground reaction force(vGRF) in

running (Oriwol and Maiwald, 2011), kinematic variability in throwing tasks (Wagner, et al., 2012), waveform variability in electromyography (EMG) signals during walking (Clancy, 1998) and variability in plantar pressure (Cavanagh, et al., 1998). The CV is a widely established calculator of variability in the clinical (Winter and Yack, 1987; Owings and Grabiner, 2003; Heiderscheit, 2000; Brach, et al., 2008) and movement sciences (Hamill, et al., 1999; 2000; Hausdorff, et al., 2000; Li, et al., 2005; Wilson, et al., 2008). The use of both calculators in chapter 17 facilitated the relative comparison of interpretations to the wider biomechanical literature.

17. The magnitude and spatial distribution of variability in plantar pressure at a wide range of walking speeds

17.1 Abstract

During walking, variability in step parameters allows the body to adapt to changes in substrate or unexpected perturbations that may occur as the feet interface with the environment. Despite a rich literature describing biomechanical variability in step-parameters, there are no studies that explore the habitual spatial distribution or magnitude of variability in plantar pressure in healthy humans. This experiment used pSPM and two standard measures of variability, the MSE and CV, to assess the magnitude and spatial distribution variability in plantar pressure across a range of controlled walking speeds. Results by reduced major axis, and pSPM regression, revealed no consistent linear relationship between MSE and speed or MSE and Froude number. A positive linear relationship however was found between CV and walking speed and CV and Froude number. The spatial distribution of variability was very different when assessed by MSE and CV: relatively high variability was consistently confined to the medial and lateral forefoot when measured by MSE, but in the forefoot and heel when measured by CV. In absolute terms, variability by CV was universally low (<2.5%). From these results, it was determined that pressure variability assessed by MSE to be independent

of changes in walking speeds, and that CV is not an accurate measure of peak pressure for this analysis of spatial variability.

17.2 Introduction

Walking is a complex task involving the coordination of multiple body segments over multiple cycles (steps) (Winter and Yack, 1987; Gates, et al., 2012; McAndrew, et al., 2011). As one of the most practiced of all motor skills (Jordan, et al., 2007) variability facilitates continuous, adaptive coordinated movement through the environment, resisting expected and unexpected perturbations that may occur causing instability (Winter, 2005; Lipsitz, 2002). Studies of variability are thus central to understanding gait stability, its development, and degeneration (Newell and Corcos, 1993; Hausdorff, et al., 2001; Beauchet, et al., 2012). Controlling speed during walking is also complex and highly variable, coordinated by interactions of the nervous and musculoskeletal systems and the environment (Meardon, et al., 2011). However, the natural waning of biological systems due pathology, disease, injury and ageing, can affect walking speed control, and is cited as an important predictor of clinical outcomes: e.g., length of stay in hospital post-stroke (Rabadi and Blau, 2005) and mortality in older adults (Ostir, et al., 2007) among others (Robinett and Vondran, 1988; Langlois, et al., 1997; McGinn, et al., 2008; Waite, et al., 2005).

Variability in kinematic parameters is not always considered beneficial, but equally some degree of variability is not always considered detrimental (Kang and Dingwell, 2008; Beauchet, et al., 2012). High variability in kinetic and kinematic variables can increase energetic costs (O'Connor, et al., 2012), and increase the risk of falls (Toebe, et al., 2012), but equally it can facilitate an increase in motor performance (Wymbs, et al., 2016). Both younger (<65 years) and older (>65 years) adults follow U-shaped curves in variability of kinematic parameters, increasing the variability at speeds faster, or slower than their comfortable walking speed (Jordan, et al., 2012), only there is a slightly wider distribution in the magnitude of kinematic variability in older adults (Kang and Dingwell, 2008). P-images capture the summation of inertial and vGRF forces produced by the moving body against the ground for each step (Cavanagh, et al., 1998). Fluctuations in the CoM over the base of support, and perturbations that challenge stability during adaptive coordination (Dingwell, et al., 2001) occur here, at the foot-ground interface, however the habitual pattern of variability in plantar pressure is not completely understood in healthy populations (Cavanagh, et al., 1998; van Emmerik, et al., 2016): for example, variability in peak plantar pressure is limited to one clinical study (Cavanagh, et al., 1998) from a cohort of patients with diabetic neuropathy using a regionalisation approach. It is therefore timely for a systematic study characterising the habitual variability of plantar pressure in healthy subjects ($n = 16$) covering the spectrum of walking speeds available and suitable to young, healthy cohorts (1.1m/s –

1.9m/s, <45years, Table 1). pSMP facilitates the analysis of the accumulated whole body variability step-to-step, from the whole pressure field of each foot-step (p-image), avoiding any potential biases associated with regionalisation techniques (Pataky, et al., 2008).

The variable nature of motor patterns and locomotion implies that each pressure record will be slightly different (Su and Dingwell, 2007; Byl and Tedrake, 2009). Cavanagh, et al., (1998) assess variability in peak plantar pressure from a total individual trial n of 50 mid-step steps, collected in sets of 10 steps from diabetic, diabetic neuropathic and non-diabetic populations in three shoe conditions (Oxford, running shoe, barefoot). The authors reported highest variability under MTH1 and the hallux. The MSE measure of variability was approximately 40% higher in the former than the latter, and when considered together were 6-12x higher than variability at the heel. A recent study of plantar pressure at a single walking speed using >500 p-images per subject, demonstrated large inter- and intra-subject (i.e. step-to-step) pressure variation in the midfoot (Bates, et al., 2013b). However, discussion of variability across the whole plantar surface, and the influence of speed were not considered as part of the study.

Here therefore, the relationship between the magnitude and spatial variability in peak pressure with a wide range of controlled walking speeds (1.1m/s- 1.9m/s), and from a large individual trial n is reported. Most previous investigations of the effects of speed on peak plantar

pressure distribution use self-selected walking speeds, described as 'slow', 'preferred and 'fast' (Abellan, et al., 2009; Henning and Rosenbaum, 1991; Hughes, et al., 1991), however speed is controlled here to standardise the comparative analysis between walking speeds. The aims of this study were to assess the effect of walking speed on the: (i); magnitude and (ii); spatial distribution of variability across the whole plantar field, and (iii), to describe the spatial distribution of variability using these two commonly used metrics in biomechanical studies, MSE and CV (Winter and Yack, 1987; Cavanagh, et al., 1998; Owings, et al., 2003; Heiderscheit, 2000; Brach, et al., 2008, Hamill, et al., 1999; 2000; Li, et al., 2005; Wilson, et al., 2008; Clancy, 1998; Oriwol and Maiwald, 2011; Wagner, et al., 2012).

17.3 Materials and methods

The dataset for this chapter is described in detail in the background to materials and methods chapters 16.1 and 16.2 is used here, and for the following three chapters. Briefly, sixteen healthy subjects (aged 21-46) with no known or prior limb abnormalities walked barefoot continuously for 5 minute periods, at 5 different speeds (1.1m/s, 1.3m/s, 1.5m/s, 1.7m/s and 1.9m/s) on a Zebris FDM-THM pressure sensing treadmill walking speeds, differing by $\pm 20\%$. All subjects provided informed consent, and procedures were approved by the University of Liverpool Research Ethics Committee (RETH 000088).

Peak pressure values were extracted from each sensor contacted by the foot on the treadmill, using a custom-written C program (Pataky, et al., 2008; Zhu, et al., 1995), yielding sixteen total individual walking speed trials ranging between 2,780-3,535 p-images per subject (Table 1). This exceeds the required individual train n of >400 steps suggested for reliability in the MSE for plantar pressure (chapter 19). P-images from each individual walking speed trial were registered in accordance to the method outlined in detail in chapter 16.2 (Pataky and Goulermas, 2008).

Intra-subject analyses using pSPM were conducted on all pressure records to quantify spatial variability in the walking speeds collected here (Pataky and Goulermas, 2008). To quantitatively assess changes in the variability of peak pressure at different walking speeds, we used two different measures of variability. The algorithm used to register p-images in pSPM is based on minimising the MSE between pixels globally, across each image. Previous studies of walking speed using pSPM have sought to test if the mean pressure across the foot differs between walking speeds (Pataky, et al., 2008). Thus, in the context of previous studies using pSPM that examine changes in pressure with speed (Pataky, et al., 2008) it is logical to assess variability relative to the mean pressure in each pixel at each walking speed.

MSE reflects the absolute variation of each pixel value to the same pixel value in the mean p-image calculated for each individual walking

speed trial. In addition, we chose to calculate the pixel-level variability by the CV, as it is a widely used measure of variability in clinical (Winter and Yack, 1987; Newell and Corcos, 1993; Heiderscheit, 2000; Dingwell, et al., 2001; Brach, et al., 2008) and sports biomechanics (Hamill, et al., 1999, 2000; Li, et al., 2005; Bartlett, et al., 2007; Wilson, et al., 2008). CV calculates the variance of the entire sample about the mean but does take into consideration the error that arises from differences in pixel vector values. However, the widespread use of CV allows us to contextualise the results presented here to other biomechanical gait parameters (e.g. step length, width, time and impulse).

MSE was calculated over non-zero pixels in each p-image within a subject's total sample according to:

$$MSE = 1/n \sum (I_{0k} - I_{kk})^2$$

where n is the total number of non-zero pixels in the mean image; I_0 is the mean of the subject's overall sample and I_k is an individual pedobarographic record. The CV was calculated over non-zero pixels in each pedobarographic image within a subject's total sample according to:

$$CV = \frac{SD}{m} * 100$$

where m is the mean value of each non-zero pixel over all pressure images in the sample, and SD is the standard deviation of the sample across all p-images in each subjects' data set. Each value is multiplied by 100 to produce a percentage classed as high ($>5\%$) or low ($<5\%$) (Beauchet, et al., 2009). Very low levels of variability are considered $<3\%$ (Jordan, et al., 2012).

The MSE and CV of each pixel in the p-image is summed to produce a total MSE and CV value for each individual pressure record, about the subject's overall mean pressure image. Each speed trial produces a different number of prints as more steps are generally taken at faster walking speeds. To standardise our comparisons of the differences between speed samples, we used a downsampling approach to extract random sub-samples of $n = 400$ p-images from the overall total individual walking speed trial n , a total of 100 times. The MSE and CV of each 100 samples of 400 prints was calculated, and a mean p-image for each individual walking speed trial was produced, and the mean value retained as representative for each walking speed. To assess changes in variability with walking speed we plotted MSE and CV against individual walking trial using reduced major axis regression (RMA), and conducted topological linear regression analysis on the MSE analysis. All image processing and analysis described above was conducted using MATLAB (MathWorks, USA).

17.4 Results

The main results of this study can be summarised as follows:

Topological linear regression analysis of MSE and individual walking speed report no statistical support for a systematic linear increase in variability with walking speed (Figure 4). RMA regression reports positive linear trends in MSE across walking speed trials in 11 out of 16 subjects, and in CV in 15 out of 16 subjects (Figure 5). However, r^2 and p values ($r^2 > 0.5$, $p = < 0.05$) only strongly support this trend in 2 subjects by MSE, but in 6 when calculated by CV (Table 2).

When walking speed was normalised by Froude number, RMA regression reported positive linear relationships between MSE and Froude number in 11 out of 16 subjects, and CV and Froude number in 15 out of 16 subjects (Figure 6). Supporting statistics however ($r^2 > 0.5$, $p = < 0.05$), only support a linear increase in MSE in with Froude number in 3 subjects, and again, in 7 subjects when assessed by CV (Table 3). The same subjects are not statistically significant across all comparisons.

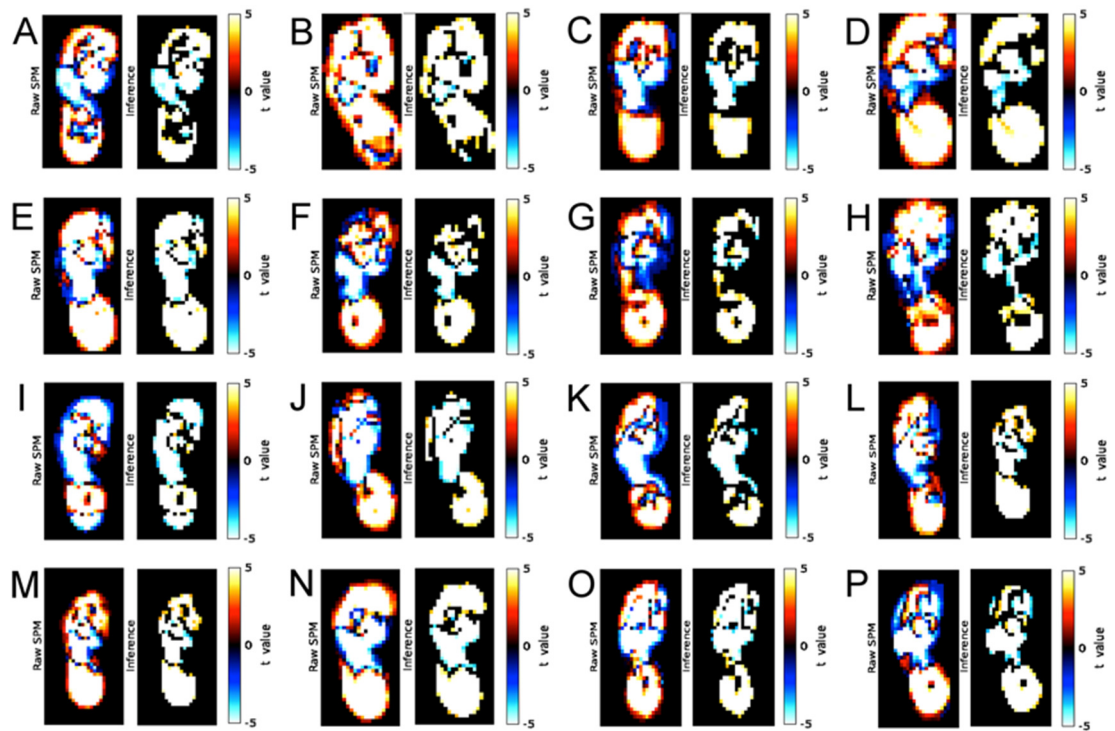


Figure 4

Linear regression analysis by pSPM extracted from the total individual trial mean p-image (left p-image), reveals no statistical support for linear changes in variability by MSE with walking speed (right p-image). The right p-image is the statistical inference map, showing areas of increasing or decreasing variability in peak pressure across the plantar surface. Red pixels indicate increasing variability with walking speed around the periphery of the heel and forefoot only. Blue pixels indicate decreasing variability with walking speed around the periphery of the midfoot and occasionally the hallux. Statistically significant pixels are concentrated almost exclusively around the periphery of mechanically distinct areas of the foot, thus they are most likely pixel artifacts relating to small changes in foot contact area, size and shape with walking speed. The mechanically distinct areas of the plantar surface; heel, mid-, forefoot, remain white indicating that no statistically significant relationships are evident between peak pressure variability and this range of walking speed.

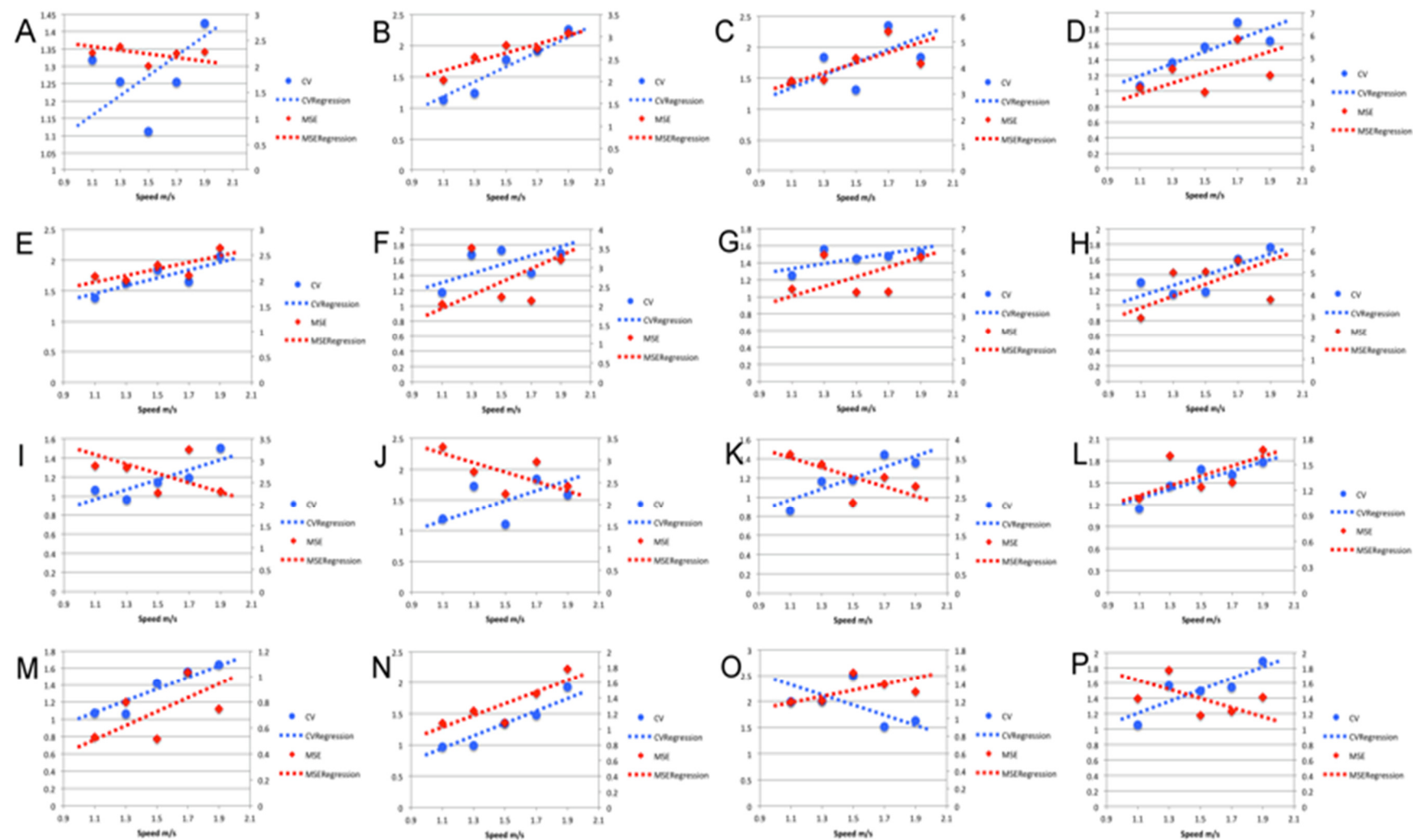


Figure 5

RMA regression suggested positive linear trends in MSE across all walking speeds in 11 out of 16 subjects, and CV and speed in 15 out of 16 subjects.

Table 2

Regression statistics reveal a linear increase in MSE with speed in only 2 subjects (B, L) ($R^2 > 0.75$). When assessed by CV, regression statistics reveal a linear increase in CV with speed in 6 subjects (B, K, L, M, N, P) ($R^2 > 0.75$). Only subject B reports statistical significance by MSE ($p = 0.05$), but reported in 5 subjects when calculated by CV (B, K, L, M, N).

Subject	Calculation	R ²	P	Slope	Intercept
A	MSE	0.010	0.871	-0.439	2.898
	CV	0.084	0.635	0.358	0.735
B	MSE	0.853*	0.024	1.242	0.776
	CV	0.962*	0.0248	1.500	-0.586
C	MSE	0.424	0.233	2.470	0.493
	CV	0.260	0.379	1.283	-0.170
D	MSE	0.173	0.484	2.950	-0.101
	CV	0.739	0.061	0.965	0.056
E	MSE	0.547	0.152	0.802	1.023
	CV	0.731	0.064	0.798	0.516
F	MSE	0.049	0.718	2.158	2.158
	CV	0.276	0.362	0.736	0.432
G	MSE	0.051	0.713	2.774	0.639
	CV	0.363	0.281	0.372	0.890
H	MSE	0.107	0.589	3.405	-0.643
	CV	0.643	0.102	0.860	0.108
I	MSE	0.081	0.081	-1.333	4.711
	CV	0.736	0.062	0.641	0.212
J	MSE	0.332	0.308	-1.337	4.742
	CV	0.200	0.450	1.039	-0.068
K	MSE	0.408	0.245	-1.549	5.353
	CV	0.802*	0.039	0.710	0.135
L	MSE	5.845	0.990	0.712	0.297
	CV	0.830*	0.031	0.785	0.358
M	MSE	0.245	0.396	0.678	-0.291
	CV	0.910*	0.011	0.856	0.067
N	MSE	0.748	0.058	0.941	-0.086
	CV	0.925*	0.008	1.252	-0.537
O	MSE	0.219	0.426	0.447	0.657
	CV	0.256	0.383	-1.219	-1.219
P	MSE	0.113	0.579	-0.740	2.507
	CV	0.763*	0.052	0.946	0.946

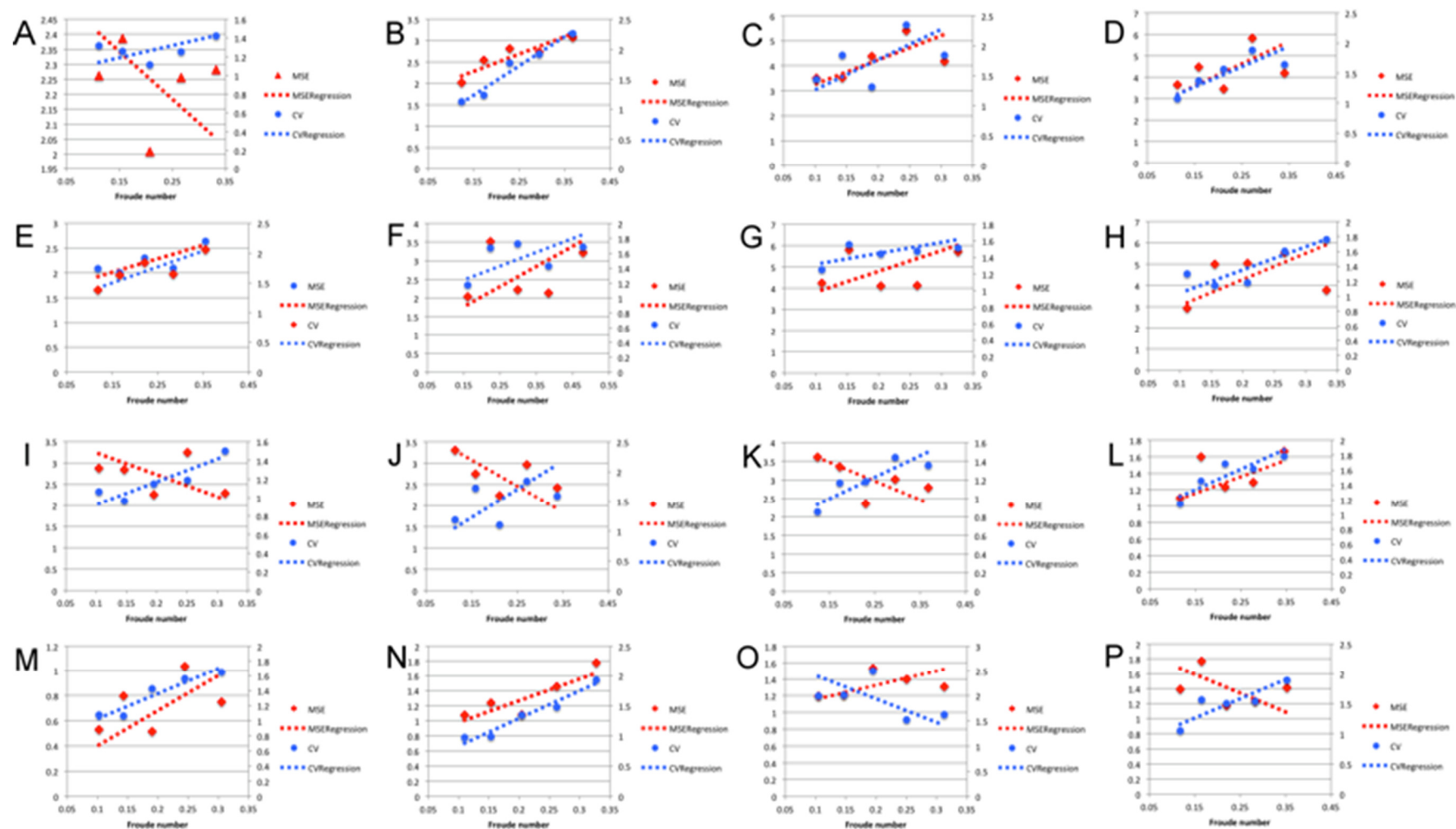


Figure 6

RMA regression reports positive linear relationships between MSE and Froude number in 11 out of 16 subjects, and CV and Froude number in 15 out of 16 subjects. r^2 and p -values ($r^2 > 0.75$, $p = < 0.05$) strongly support linear increases in variability with Froude number in only 4 subjects when assessed by MSE, and in 11 subjects when assessed by CV (Table 3).

*Froude number is ($Fr = v^2/g*LL$). Where, v^2 is speed squared, g is gravity ($9.81m/s^2$), and LL is each subject's leg length measured from the superior apex of the iliac crest to the where the heel meets the floor.*

Table 3

Regression statistics reveal a linear increase in MSE with Froude number in only 3 subjects (Subjects B, M, N). When assessed by CV, regression statistics reveal a linear increase in CV with speed in 7 subjects (Subjects B, F, I, K, L, M, P).

Subject	Calculation	R ²	P	Slope	Intercept
A	MSE	0.004	0.914	-1.587	2.580
	CV	0.128	0.129	1.293	0.996
B	MSE	0.815*	0.036	4.050	1.679
	CV	0.959*	0.004	4.891	0.502
C	MSE	0.381	0.267	9.701	2.286
	CV	0.253	0.388	5.041	0.761
D	MSE	0.159	0.506	10.397	2.039
	CV	0.680	0.086	3.402	3.402
E	MSE	0.591	0.591	2.712	1.606
	CV	0.721	0.069	2.696	2.696
F	MSE	0.052	0.712	5.413	5.413
	CV	0.956*	0.237	0.406	0.968
G	MSE	0.121	0.121	0.566	9.770
	CV	0.300	0.300	1.311	1.187
H	MSE	0.066	0.066	12.268	1.828
	CV	0.704	0.076	3.098	0.732
I	MSE	0.093	0.619	0.619	3.759
	CV	0.794*	0.042	2.459	0.678
J	MSE	0.268	0.268	-6.088	3.984
	CV	0.238	0.404	4.732	0.520
K	MSE	0.361	0.361	0.284	-5.051
	CV	0.752*	0.057	2.316	2.316
L	MSE	0.000	0.975	2.010	0.855
	CV	0.782*	0.046	2.724	0.929
M	MSE	0.929*	0.432	2.795	0.122
	CV	0.903*	0.903	3.364	0.689
N	MSE	0.789*	0.789	2.875	0.691
	CV	0.691	0.004	4.588	0.372
O	MSE	0.174	0.484	1.715	0.982
	CV	0.292	0.348	-4.677	2.873
P	MSE	0.105	0.594	-2.515	1.970
	CV	0.745*	0.060	3.214	0.775

The magnitude of variability in plantar pressure by MSE and CV is high (Figure 7, 8 Table 4) but localised (Figures 7, 8), both within and between walking speed trials, and between subjects. All subjects expressed a total individual trial CV <2.5% (Figures 5, 6). Qualitative analysis of topological variation maps suggests that spatial distribution of MSE is highest in the under MTH5 and MTH1 respectively in all subjects,

and is independent of walking speed (Figure 7). Qualitative analysis by variation maps suggests that the spatial distribution of CV is highest in the midfoot, medial phalanges, big toe and lateral margins of the heel in all subjects, and is dependent on speed (Figure 8).

Table 4

Subjects with the highest (G and D), average (I) and lowest (M) MSE at each walking speed, and the total combined MSE.

Subject	MSE 1.1m/s	MSE 1.3m/s	MSE 1.5m/s	MSE 1.7m/s	MSE 1.9m/s	Total MSE
G	4.244	5.809	4.107	4.136	5.711	4.801
D	3.649	4.479	3.459	5.821	4.208	4.323
I	2.885	2.848	2.267	3.255	2.300	2.711
M	0.531	0.800	0.516	1.036	0.749	0.726

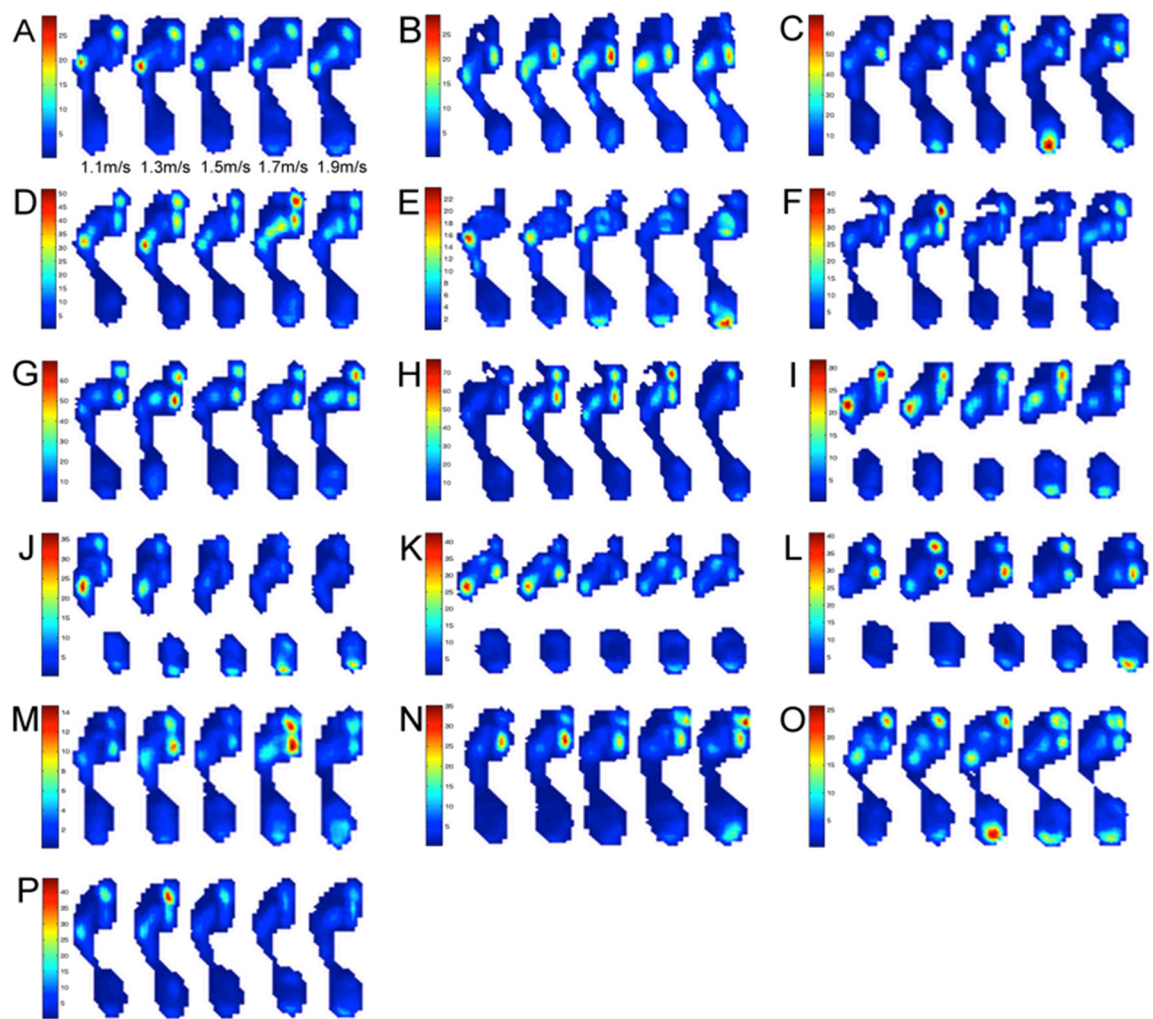


Figure 7

MSE variation maps report the distribution and magnitude of the combined MSE in each pixel from the individual walking speed trial mean *p*-images in all subjects. Intra-subject spatial variability is highest, and confined almost exclusively to under MTH5 and MTH1, and no consistent increasing or decreasing relationship with walking speed.

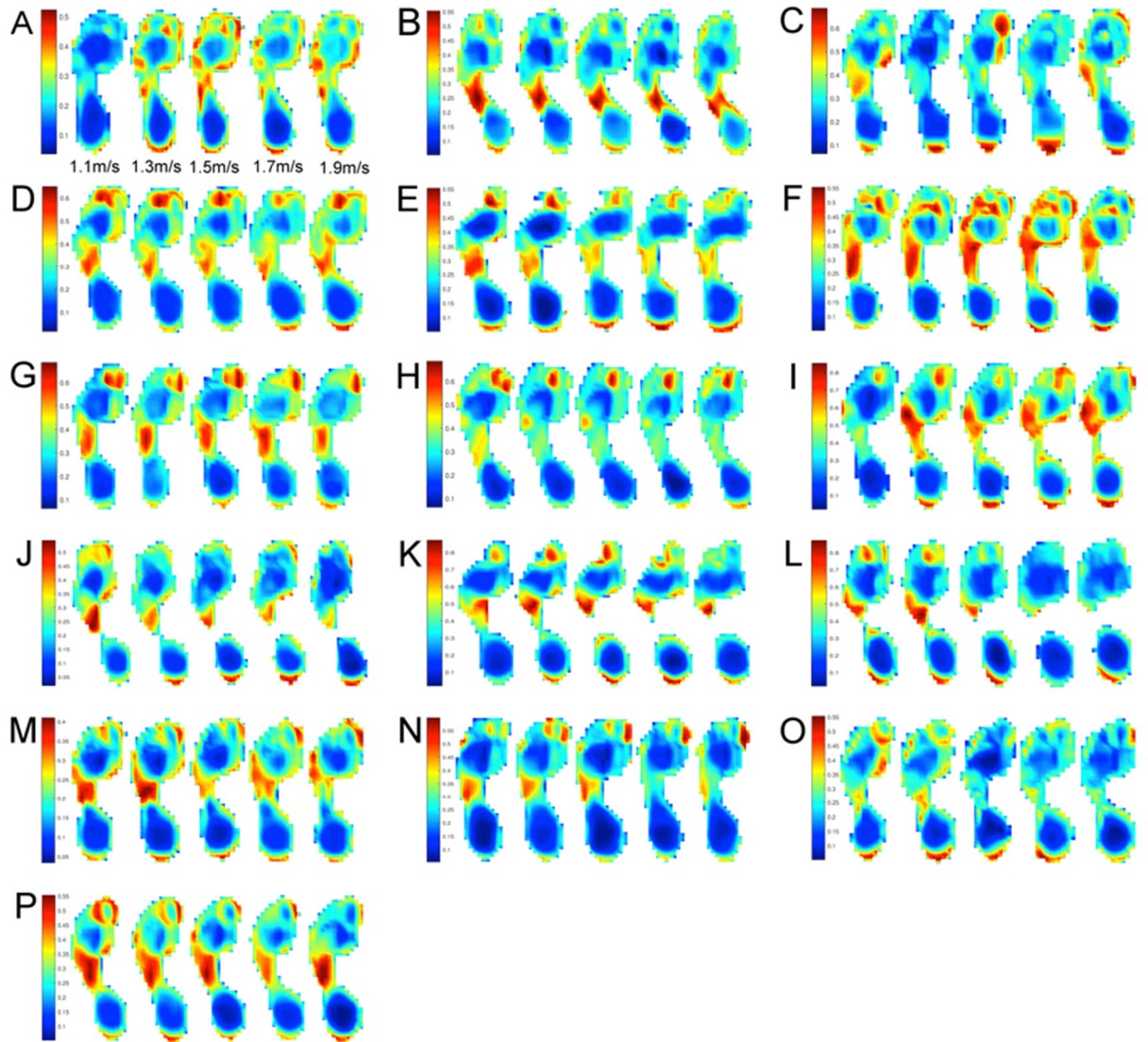


Figure 8

CV variation maps report the distribution and magnitude of the combined CV from each pixel from the individual walking speed trial mean p-images in all subjects. Intra-subject spatial variability is highest and localised under the hallux, medial phalanges, and midfoot. No consistent increasing or decreasing relationship is evident with walking speed.

17.5 Discussion

Variability is a fundamental feature of all biological systems (Glazier, et al., 2006; Gaudez, et al., 2016) and this contribution represents the first attempt to quantify variability in plantar pressure from the whole pressure field, and to establish its relationship with walking speed in healthy subjects. The pSPM analysis was conducted on a large total individual trial n , and individual speed trial n . These two features of the analysis helped to remove any potential bias that might arise from a regionalisation approach (Pataky et al. 2008), or elevated measures of variability associated with small sample sizes (Dingwell, et al., 2001; Owings and Grabiner, et al., 2003; Hollman, et al., 2010; van Schooten, et al., 2012; Riva, et al., 2013). The whole pressure field analysis by pSPM did not denote any statistical support for an increasing or decreasing linear relationship between MSE and walking speed (Figure 4). The two measures of variability also produced directly contrasting results (Figures 7, 8). The implications of this study are that variability in plantar pressure does not follow the commonly reported U-shaped distribution in other lower limb kinematic parameters (Winter and Yack, 1987; Jordan, et al., 2007; Kang and Dingwell, 2008; Beauchet, et al., 2009; Dingwell, et al., 2001, 2010; Dingwell and Cusumano, 2015), when walking faster or slower than a comfortable walking speed.

17.5.1 Magnitude of variability

The inter-subject range of variability in MSE is high. For example, the subject with the highest MSE was 9.8x more variable than the subject with the lowest MSE at 1.5ms (Figure 4, Table 4). The subject with the highest CV was 2.3x more variable than the subject with the lowest CV at 1.5ms (Table 4). The large inter-subject variation in MSE and CV is striking given our relatively homogeneous cohort of healthy adults, who ranged from 21-44 years old with no pathology or pre-existing injuries and a low BMI. CV <5% in kinematic step-parameters is considered low (Winter and Yack, 1987; Kang and Dingwell, 2008; Heiderscheit, 2000; Beauchet, et al., 2005, 2007, 2009; Hausdorff, 2007; Owings and Grabiner, 2004), and <3% very low (Jordan, et al., 2007). Here, we found the plantar pressure CV to be universally low i.e., <2.5% in all subjects (Figures 5, 6). This characteristic, and the lack of statistically significant correlations between variability and walking speed is consistent with the analysis by Cavanagh and colleagues (1998). However, comparisons are not made directly to this clinical trial due to the incomparable differences between populations, and the results are reflective only of this sample of volunteers. Universally low CV is likely the product of the artificial effects of treadmill walking, that reduce the natural stride-to-stride variability in kinematic patterns (Nelson, et al., 1972; Wank, et al., 1998; Dingwell, et al., 1999). Further, the treadmill acts to stabilise kinematic variability, and reduce system sensitivity to perturbations, reducing the variability, and leading to a more stereotypical motor pattern response within the 5-

minute periods of walking trials. Even at fast speeds (1.9m/s) – very close to the physiologically threshold for the walk-run transition at 2.0m/s and where walking mechanics could theoretically be compromised, variability remains very low and shows no relationship to the system's attempts to maintaining a very fast, and energetically inefficient walking speed. Near the walk-run-walk transitions, stride duration increases before and after the transition (Jordan and Newell, 2008), and increases at slower walking speeds (0.2-0.6m/s) compared to speeds between 0.8-1.6m/s. A linear increase in variability is present in joint angles (Brisswalter and Mottet, 1996), step length (Beauchet, et al., 2009), step time interval (Owings and Grabiner, 2004) and step impulse (Winter and Yack, 1987).

Characteristically low variability is compounded further by the high functional redundancy in the foot complex, defined by an abundance of degrees of freedom (DoF). Variability in plantar pressure is naturally low to coordinate the multiple available degrees of freedom in the foot, accounting for potential changes in substrate compliance, direction, speed and slope: all inevitable features of locomotion (Heiderscheit, 2000). Controlled speed on a treadmill and thus, full sensorimotor awareness that there will be no expected or unexpected changes in speed, substrate or direction, increases the pattern coordination of redundant degrees of freedom during normal walking, maintaining low variability. Each step cycle is thus assembled temporarily, but flexibly, to facilitate adaptability, and maintain balance and stability (Turvey, 1990). It has been shown that

when the sensorimotor system adopts functionally preferred states of coordination between soft and hard tissues, it is ordered and stable, reflecting consistency in motor patterns (Kelso, 1995) and thus low variability.

While the result presented here is perhaps expected, it is potentially more unanticipated in Cavanagh and colleagues' (1998) cohort considering the reduced sensorimotor feedback response at the plantar surface due to neuropathy. The authors predicted the lack of any significant changes in variability were due to a low individual trial n (50 steps of 10 steps) that was not sufficient to cause trauma to the plantar surface, and stimulate a change in variability in peak pressure (Cavanagh, et al., 1998). These results do not lend support to clinical trials, however they do provide valuable insights into the neurological mechanisms driving change in plantar pressure, and should be explored in over-ground long distance walking over irregular terrain (Winder, et al., 2015; Allen, et al., 2016). That variability is independent of speed supports Cavanagh et al. (1998), in that variability was also not a discernible parameter signifying change in shoe type, or able to distinguish between diagnostic populations. The two studies are similar in their application of MSE and CV as calculators of variability to peak plantar pressure. The studies differ in: (i) method i.e., mid-gait pressure in-sole data collected overground vs. continuous pressure sensitive treadmill, (ii) sample characteristics i.e., diabetic and diabetic neuropathic vs. non-pathological (iii) individual trial

n i.e., 50 p-images per condition vs. >400 p-images per speed, and (iv) experimental conditions i.e., shoe type and diabetic neuropathy vs. walking speed. The studies also differ in analysis, i.e., regionalisation vs. pSPM. Despite the differences in the test methodologies and analyses, , both studies confirm no discernible trends in variability in plantar pressure between speed, shoe condition, or between diagnostic cohorts (Cavanagh, et al., 1998). However, variability was significantly higher in regions where frequent ulceration is common under the MTH1 and hallux (Cavanagh, et al., 1998). Cavanagh et al. (1998) suggested that future studies should attempt to collect greater numbers of steps, in order to validate their findings, however we do not validate them here completely due to differences in experimental protocol.

Specifically, Cavanagh and colleagues (1998) reported highest variability in the medial forefoot specially under MTH1 and the hallux (MSE approximately 40% higher in the former than the latter), which is 6-12x higher than variability at the heel. The authors attribute this to the functional role of the “medial column” during walking (pg. 197, Cavanagh, et al., 1998), and the high propulsive forces generated at these units during the final part of stance phase. Despite differences in method, analysis, conditions and population, these results are confirmed here, with the addition of high variation also observed consistently across speeds in the lateral forefoot under MTH5 when calculated by MSE (Fig 7). Figure 7

reveals highest variability occurs most consistently in MTH5, MTH1 and the hallux, and is independent of walking speed.

17.5.2 Variability-speed relationship

Results show that variability in plantar pressure does not follow the same U-shaped curve relationship with speed, as do other lower limb step kinematic parameters. Here, the RMA regression statistics support an increase in MSE with speed in only 2 out of 16 subjects, but in 6 out of 16 subjects when assessed by CV ($r^2 > 0.75$, $p = < 0.05$) (Table 2, Figure 5). When speed was normalised by Froude number, statistically significant linear increases in MSE with speed were also only evident in 3 subjects, but in 7 out of 16 subjects when assessed by CV ($r^2 > 0.75$, $p = < 0.05$) (Table 3, Figure 6). Almost all the same subjects had strong statistical evidence for changes in pressure with increasing speed (Tables 2, 3) however subjects were not consistently the same across speed or by Froude number. All 4 subjects who exemplify strong supporting statistics showed an increasing linear relationship between variability in plantar pressure and walking speed when assessed by CV (Tables 2, 3) (Figures 5, 6).

The general lack of linear relationship was confirmed by topological pixel-by-pixel regression analysis of MSE versus speed using pSPM, that revealed no statistical support for a linear increase or decrease in MSE with speed (Figure 4). Only pixels at the outer margin of the foot

showed strong statistical linear trends, as a direct result of small changes in foot area contact size and shape that occurs step-to-step at very different speeds. Specifically, the red margins of the left inference prints in Figure 4 indicate an increase in MSE with speed around the periphery of the heel and forefoot, while the blue margins indicate a decrease in MSE with speed around the periphery of the midfoot. It is likely that this significant relationship reflects changes in pressure or contact area increasing with speed in the forefoot and heel, and decreasing in pressure or contact area in the midfoot as speed increases. These artifacts could be removed by use of a non-rigid body image registration approach as discussed in chapter 16.2.

17.5.3 Spatial distribution of variability

Finally, this contribution presented a novel means of analysis of quantifying the spatial distribution of step-to-step variation in whole pressure fields, using both MSE and CV metrics. Using pSPM, we visualized variability in plantar pressure distribution producing variation maps that plotted the MSE and CV of each pixel, and the datasets combined to produce a mean image within the total individual trial n , and combined the means to represent one print for each speed (Figures 7, 8). MSE variation maps show centres of highest variation to be favourably localised under the lateral and medial MTHs 5 and 1 (Figure 7). However, equally, by the same qualitative assessment, CV variation maps show that the centres of

highest variation lay more generally under the midfoot and phalanges (Figure 8).

This disparity may be largely explained by the differences between the two metrics and the ‘typical’ distribution of peak pressure across anatomical regions of the foot. MSE directly reflects the tendency for absolute peak pressure values to vary about the sample’s absolute mean value, and may therefore be slightly susceptible towards bias indicating higher variation in areas of high absolute pressure. By contrast, CV represents a normalised measure of variability and shows a strong preference towards highlighting areas of low mean pressure as being highly variable (e.g., Cavanagh, et al., 1998). This generally explains why high CV values (red) are evident around the periphery of the foot and within the midfoot, and lower CV values (blue) are clustered where areas of high pressure exist, namely at the heel and forefoot (Figure 8).

Although MSE and CV appear qualitatively to paint opposing pictures of spatial variation, it is possible that the step-to-step variations they highlight are not biomechanically contradictory. A recent study found that pressure in the lateral forefoot was higher in steps where mid-foot pressure was also elevated; and conversely that the same subjects exhibited statistically significant increases in pressure in the medial forefoot and hallux in steps where midfoot pressure was low (Bates, et al., 2013b). Consistent with the latter finding, Stolwijk and colleagues (2013)

found that Malawian subjects with anatomically and/or functionally flatter feet also exhibited a more laterally placed CoP in late stance. It is therefore possible that the variability in the mid-foot highlighted by CV maps (Figure 8) is functionally correlated to the forefoot variation seen in MSE variation maps (Figure 7), in terms of varying paths of the CoP in mid- to late-stance. Such a relationship would imply that the function of the midfoot and MT1 and 5 are highly interdependent.

Until we can obtain large samples of coronal transverse vGRF curves, we cannot draw firm conclusions. We suggest however that theoretically, such a scheme of variability in mid- and forefoot pressure might reflect a biomechanical function for controlling perturbations in late stance in the coronal plane, through internal/external foot rotation step-to-step. This is only an assumption however, and requires the application of stability measures to pixel vectors, and is a potentially exciting avenue to explore, particularly over uneven terrain. It is further possible that spatially consistent high variability in peak pressure relates to the mechanical influence of a tunable gearing ratio within the foot (Carrier, et al., 1994): that is, the changing relative lengths of the muscle lever arm, and the load lever arm measured from the CoP. Pre-tensioning, the effect of dorsiflexion at the talocrural joint on the PA prior to heel-strike (Caravaggi, et al., 2010), followed by a stretching of the PA around the metatarsal heads during toe-off (the windlass mechanism) (Ker, et al., 1987), contributes to increased stiffening of the plantar soft tissues, and

thus, increases the gear ratio at late stance (Carrier, et al., 1994), when the CoM is over the forefoot. *During the time series of a foot cycle, inaccuracies in interpreting the variability in the path of the CoP are high because of low pressures exerted on the force plate during heel strike and toe-off. Variability can reveal error in order of 2%, thereby increasing the inaccuracy of the measure during these phases.* Hypothetically, it may be possible that the combined variation in gearing (Carrier, et al., 1994) and local stiffness (Daley, et al., 2007) - with a potentially substantial contribution of varying tension of the transverse and oblique heads of abductor hallucis (Jung, et al., 2011; Kelly, et al., 2012), could also be contributing to confined spatial variability, and, to the extent to which medio-lateral transfer of pressure in late stance is achieved (Kelly, et al., 2012) (Figure 7). These assumptions cannot be tested without analysis of a similar sized dataset during overground, or uneven terrain walking.

17.5.4 Future directions

This study offers a quantitative and qualitative description of not only the observed variability in peak plantar pressure, but also the effect that speed has on the magnitude and spatial distribution of variability across continuous pressure fields. An extension of Cavanagh and colleagues (1998) analysis of variability in peak pressure in patients with diabetic neuropathy, during everyday activities, to define the sensorimotor mechanisms underlying pathology would be a logical first step from this project. Tunable gearing in children under five has been

shown to mature quite late; and children have consistently low forefoot plantar pressures compared to adults (Henning and Rosenbaum, 1991), with late development of the medial-to-lateral transfer of the centre of pressure (Henning, et al., 1994). Functionally, the forefoot delivers propulsive force from the hind- to the forefoot, facilitating toe-off: however, before 7-8 years of age, accelerative power is driven from the hind- and midfoot (Li, et al., 1996). That we found variability in peak pressure is highest in the forefoot in the lateral and medial forefoot (assessed by MSE), and more generally in the forefoot (assessed by CV), is consistent with the findings of Li and colleagues (1996) and would be an interesting future direction for this research (Henning, et al., 1994). Finally, a similar analysis should be completed during non-treadmill walking at comfortable walking speeds, and on uneven terrain, to ascertain whether variability increases or decreases when speed is not controlled, thus testing dynamic system theory.

17.6 Conclusions

Two measures of variability were used in this paper; one, a standard mathematical formula to assess variability (MSE), and another a measure commonly applied to clinical questions (CV). We conducted experiments solely on healthy young subjects, observing highest variability consistently confined to the medial and lateral forefoot as assessed by MSE, and universally low levels of variability (<2.5%) (Figures

5, 6) in the forefoot and heel as assessed by CV. From these results, we suggest that the magnitude of CV is generally dependent on walking speed, while the spatial distribution of MSE shows independence from speed. This paper presents the first attempt to understand the relationship between variability in peak pressure distribution and magnitude and speed. Functional variability and high functional redundancy are products of an adaptive biomechanical system driven by patterned motor control, however the lack of statistical relationships reported here suggest that variability in peak pressure is unlikely to be a useful indicator of change in biomechanical signal, due to the highly adaptive, complex and variable nature of the structure, and of biomechanical feedback.

18. Analysis of large datasets confirms changes in plantar pressure patterns are not as responsive to small differences in speed in healthy adults

18.1 Abstract

Reported increases in peak plantar pressure with walking speed are typically regionalised to the heel and forefoot, with decreases in the midfoot. However, small individual trial n collected mid-gait rather than continuously, and analysis by regionalisation of the plantar surface, rather than as a continuous pressure field, limit our quantitative understanding of how functional changes in pressure respond to walking speeds. In this study, a large individual trial n of between 2,780-3,535 per subject during a wide range of walking speeds available to healthy adults was collected, for an extended examination of this functional relationship using pSPM. We conducted both discrete and continuous comparisons using topological statistics, assessing mean and peak pressure across the plantar surface and subjectively in the midfoot. Pedobarographic statistics by linear regression confirmed increasing linear relationships between peak pressure and walking speed under the proximal and distal areas of the plantar surface, with high intra-subject variability. Uniquely however, the trend is more complex, as individual pressure patterns reveal this overall trend outside of traditionally accepted regionalised boundaries. A general linearity is observed when discrete scalar parameters were plotted by

RMA regression, however these were not strongly supported by r , r^2 or p -values. Indeed, when analysed at the pixel-level, statistically significant changes were only identified anterior of the heel when the most disparate speeds were compared (e.g., 1.1m/s vs. 1.7m/s). Consistency in peak pressure at similar speeds, may reflect consistency in motor pattern behaviour expected for treadmill walking. Differences in the mid- and forefoot likely reflect highly variable soft tissue tuning of the foot complex.

18.2 Introduction

Statistical analyses of p-images customarily extract discrete variables such as peak and mean pressure from pre-defined regions of the foot (Rosenbaum, et al., 1994; Taylor, et al., 2004; Barn, et al., 2016). However, regionalisation approaches can inflate, or even reverse statistical trends present in whole pressure fields (Pataky and Goulermas, 2008). The advent of SPM techniques for plantar pressure allows the spatial reconstruction of p-images and statistical inference of the whole pressure field (Friston, et al., 1995). P-images are a direct reflection of the neuromuscular control patterns of the ankle flexors and extensors (Winter & Yack, 1995), as they load and unload the foot complex against the ground (Caravaggi, et al., 2016). However, many gait studies are comprised of low individual trial $n < 50$ p-images (sometimes < 10) (see: chapter 19), consequently reducing the strength of the habitual biomechanical signal seen in gait parameters (Dingwell, et al., 2001;

Owings and Grabiner, 2003; Hollman, et al., 2010; van Schooten et al., 2012; Riva, et al., 2013).

Walking speed is controlled by a combination of feedback from the vestibular and sensorimotor systems, and 'self-organising' pattern coordination (Turvey, 1990). The ability to control and maintain a range of speeds is a marker of sound neuromuscular control (Jordan, et al., 2007a), while a lack of control over speed is a marker for neuromuscular decline, risk of falls, and of morbidity in older adults (>65) (McGinn, et al., 1998; Waite, et al., 2005; Studenski, et al., 2011). The experimental components of clinical trials vary widely: e.g., individual trial n , experimental condition, diagnostic groups, methodologies and analysis. Regardless of uniqueness however, a linear trend in pressure with speed has emerged in the literature, reporting overall percentage increases in whole plantar pressure under the heel and forefoot with speed (Hughes, et al., 1991; Rosenbaum, et al., 1994; Zhu, et al., 1995; Kernozek, et al., 1996; Brown and Mueller, 1998; Drerup, et al., 2001; Burnfield, et al., 2004; Segal, et al., 2004; Taylor, et al., 2004; Warren, et al., 2004; Yang, et al., 2005; Shu, et al., 2010), and decreases in the midfoot with speed (Brown and Mueller, 1998; Pataky, et al., 2008). All these studies included find an increase in pressure under the heel with speed. However, more variable behaviour is reported in pressure in the mid- and forefoot regions in relation to the whole plantar surface changes in pressure with walking speed: e.g., studies variously report increases (Hughes, et al., 1991),

decreases (Rosenbaum, et al., 1994; Pataky, et al., 2008) or neither, in the lateral and medial midfoot (Rosenbaum, et al., 1994; Kernozek, et al., 1996; Drerup, et al., 2001; Segal, et al., 2004; Taylor, et al., 2004, and the same is reported in the forefoot (Kernozek, et al., 1996; Segal, et al., 2004).

This chapter presents a comprehensive quantitative analysis of changes in peak and mean pressure with a range of treadmill walking speeds. Potential sampling biases were removed by the standardisation of treadmill walking speeds, a large individual trial n (>500 records), and discrete parameters quantified from the entire pressure field.

18.3 Materials and methods

18.3.1 Data collection

The dataset is described in detail in chapter 16.1 and 16.2, and thus only a brief description is given here and below. A total of sixteen subjects (11 males, 5 females aged 21-47 years; Table 1), without pathologies, abnormalities or injuries, walked barefoot on a Zebris FDM-THM plantar pressure sensing treadmill at controlled speeds of 1.1m/s, 1.3m/s, 1.5m/s, 1.7m/s and 1.9m/s for five minutes in a randomised trial order. The slowest speed (1.1m/s) was selected as slower than a 'comfortable' walking speed for healthy, cohorts 20-69 years old (Bohannon and Andrews, 2011). While control of speed is directly related to morbidity in

older and frail adults (McGinn, et al., 2008; Waite, et al., 2005) our cohort is comprised of young (<45years, Table 1) and healthy adults who could walk comfortably at all the speeds included in this analysis. The fastest speed, 1.9m/s, was chosen as the closest speed to the mean walk/run transition in healthy adults, after which walking becomes economically inefficient (at 2.0m/s) (Margaria, 1976). To assess the sensitivity of variability to speed within this range for healthy adults, speed increased in increments of 0.2m/s (1.3m/s 1.5m/s and 1.7m/s). All procedures were subject to informed consent after approval by the University of Liverpool Research Ethics Committee (RETH000088).

18.3.2 Data analysis

As described in chapter 16, peak pressure records were extracted from the pressure-time data using a custom-written C program that produced between 2,780-3,535 pedobarographic images (p-images) per subject across the five speed trials (Table 1). All p-images were then registered to each other using an algorithm that minimized the mean squared error (MSE) between the images, such that homologous structures optimally overlap (Pataky & Goulermas, 2008). Specifically, a two-stage rigid body transformation registration was performed. Initially, the first pressure record from each subject's five walking trials were used as the registration template to which subsequent images from each trial were registered. The mean image of each speed trials registered data set was then calculated and used as the registration template for a second

registration iteration (Pataky, et al., 2008). Data collection was triggered on the 11th step, and as a further guarantee of reliability, the first two steps collected were eliminated. Thus, the 11th step was taken as the template for registration (chapter 16.1 and 16.2).

Intra-subject analyses using pSPM approaches were conducted on all p-images to test for differences in the distributions and magnitude of peak pressure between walking speeds. SPM{t} significance was assessed using the critical t threshold that $\alpha = 5\%$ of the foot's pixels would be expected to reach, simply by chance, given the underlying field smoothness (Pataky and Goulermas, 2008). A combination of discrete (mean and peak values and RMA linear regression) and topological (pSPM) analyses were used to examine changes in pressure with speed. First, statistical analyses were conducted using a whole plantar surface linear regression model (Pataky, et al., 2008), (Pataky and Goulermas, 2008). Second, pixel level comparison was carried across all speeds collected (1.1m/s vs. 1.3m/s, 1.1m/s vs. 1.5m/s, 1.1m/s vs. 1.7m/s, 1.1m/s vs. 1.9m/s, 1.3m/s vs. 1.5m/s, 1.3m/s vs. 1.7m/s, 1.3m/s vs. 1.9m/s, 1.5m/s vs. 1.7m/s, 1.5m/s vs. 1.9m/s, 1.7m/s vs. 1.9m/s) within subjects.

Discrete values of average mean and peak pressure from the mean p-image of each individual walking speed trial were also calculated to examine how these simple metrics change with speed. The same metrics

were also calculated for the midfoot in isolation by subjectively defining the midfoot region of each subject's mean print per speed trial, according to the method of Bates, et al., (2013b). Subjective regionalisation was chosen for comparability with other studies who directly distinguish the midfoot (e.g., Rosenbaum, et al., 1994; Pataky, et al., 2008; Bates, et al., 2013). To examine how midfoot pressure changed relative to the rest of the plantar surface with walking speeds we also normalised the mean midfoot pressure by the plantar surface mean pressure, and peak midfoot pressure by the plantar surface peak pressure. All image processing and analysis described above was conducted using MATLAB (MathWorks, USA).

18.4 Results

18.4.1 Topological analysis of peak pressure and walking speeds

Topological linear regression of peak plantar pressure and walking speed accurately represents the linear pressure behaviour with all walking speeds revealing three distinct characteristics. Linearly increasing pressure with speed at the heel, and at the distal forefoot is strongly supported in 15 of the 16 subjects, a finding that is consistent with previous literature (Figure 9). Linearly decreasing pressure with speed is also reported in the whole midfoot, lateral, and whole proximal forefoot, and includes combinations of all and none of these in different subjects

(Figure 9). Despite high variability a generalised linear trend is evident: increasing peak pressure clustered under the heel, decreasing longitudinally and transversely at the tarsometatarsal joints and along the MT diaphyses, continuing to decrease under MTHs 5-3 in varyingly distributed clusters in 15 out of 16 subjects. Increasing peak pressure under MTH1 are reported in 10 out of 16 subjects (B, D, E, I, K, L, M, O, P), just over half the sample, but increases in pressure with speed were identified under the phalanges in all subjects.

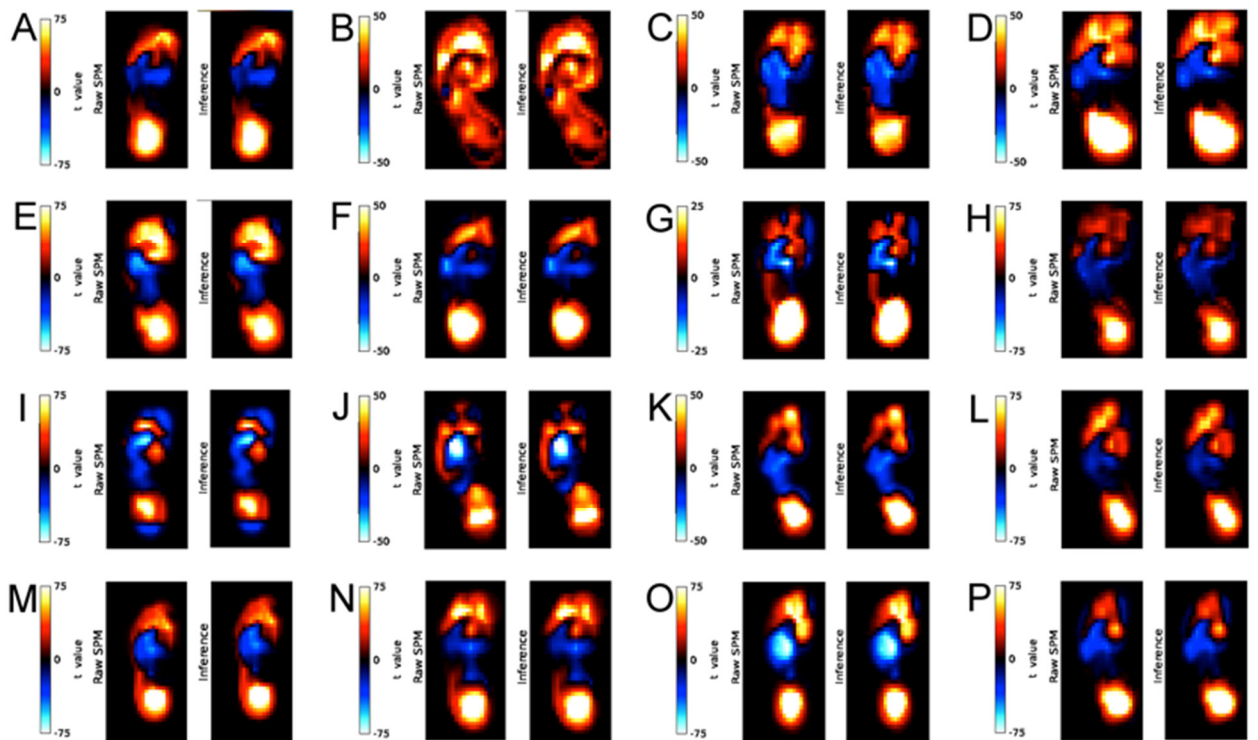


Figure 9

Linear regression analysis reveals strong increasing and decreasing linear relationships between overall plantar pressure and speed in all subjects A-P, increasing pressure with increasing walking speed are indicated by red clusters, and decreasing pressure indicated by blue clusters.

Discrete pixel-by-pixel analysis of topological changes in peak pressure with walking speed using pSPM, revealed statistically significant differences most consistently in the heel at all walking speeds, but not in all subjects (Figure 10, see: supplementary material: Figures S17.1-S17.11). Statistically significant differences in midfoot and forefoot pressure with speed were only evident at walking speeds of largest disparity, e.g., 12 subjects (A, B, C, D, E, F, I, L, N, O, P) report significant differences in peak pressure with speed in the mid- and forefoot when, e.g., 1.1m/s and 1.9m/s were compared. Significant differences in the same regions occur in fewer subjects at slightly more similar speeds, e.g. 1.1m/ and 1.7m/s in 7 subjects (D, E, I, L, M, N, O) and 1.3m/s and 1.9m/s in 5 subjects (B, E, I, J, O) (Figure 10, see: supplementary material, Figures S17.3, S17.4, S17.7).

Table 5

Subjects with the highest (D and E), average (I) and lowest (M) maximum pressure values at each walking speed, and the subjects total combined maximum pressure.

Subject	MaxP 1.1m/s	MaxP 1.3m/s	MaxP 1.5m/s	MaxP 1.7m/s	MaxP 1.9m/s	Total MSE
D	25.04	30.09	28.73	36.73	33.37	30.75
G	30.65	33.62	36.79	36.46	41.68	35.84
I	23.73	23.91	23.89	31.89	33.95	27.47
M	18.10	20.66	20.65	28.32	30.62	23.67

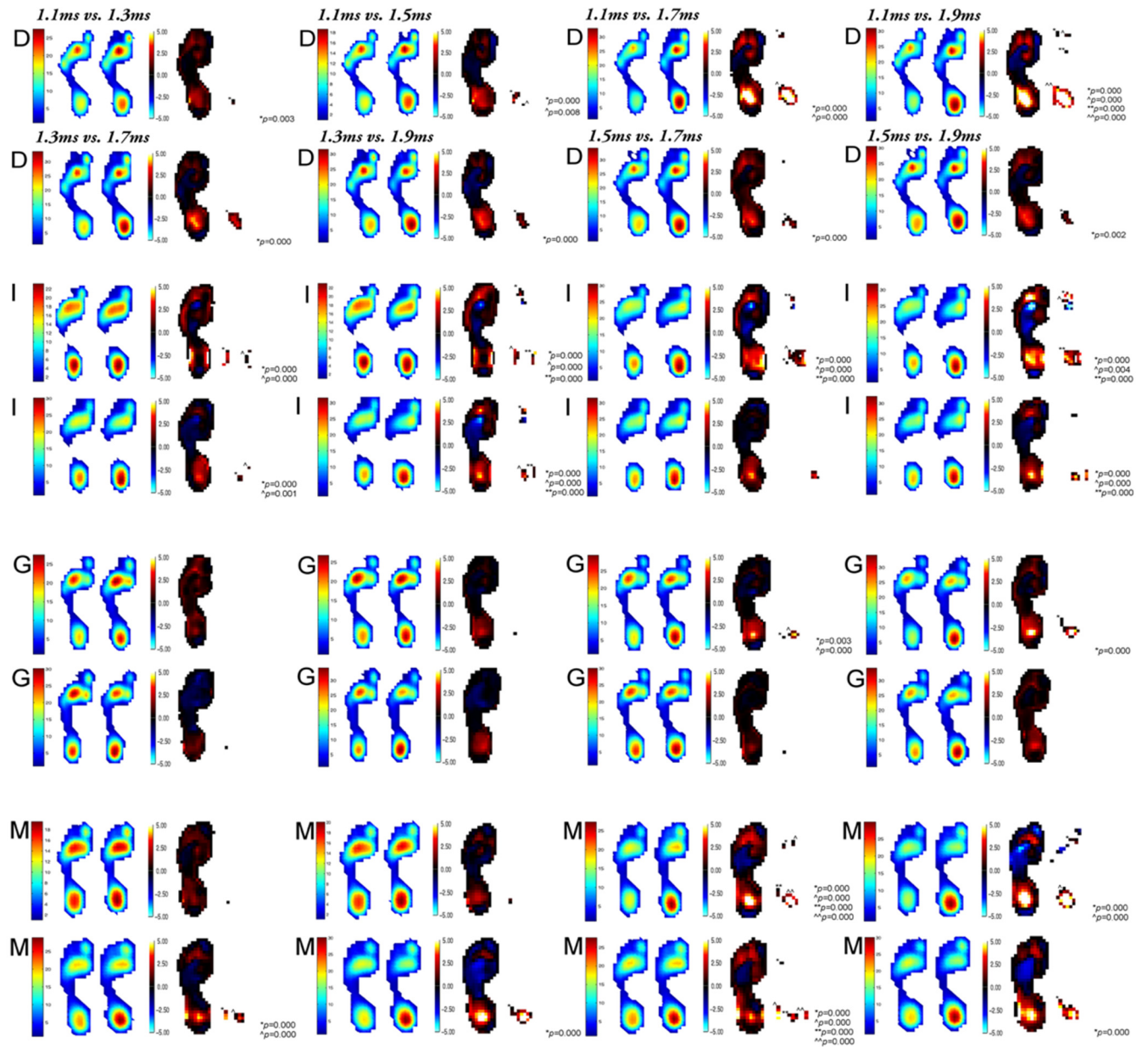


Figure 10

Discrete statistical analysis by pSPM of differences in plantar pressure magnitude when all walking speeds are compared to each other. Subject D expresses statistically significant differences between walking speeds in 8/10 comparisons (1.1m/s vs. 1.3m/s, 1.1m/s vs. 1.5m/s, 1.1m/s vs. 1.7m/s, 1.1m/s vs. 1.9m/s, 1.3m/s vs. 1.7m/s, 1.3m/s vs. 1.9m/s, 1.5m/s vs. 1.7m/s, 1.5m/s vs. 1.9m/s), and the third highest overall maximum pressure (N30.75).

Subject I express the second highest occurrence of statistically significant differences in 7/10 comparisons but with a much lower mean maximum pressure (N27.47). For comparison, subject G has the highest mean maximum pressure (N35.84), yet statistically significant differences only occur twice when the most disparate walking speed were compared (1.1m/s vs. 1.7m/s and 1.1m/s vs. 1.9m/s). The subject with the lowest mean maximum pressure (M, N23.67) reported statistically significant differences in speed comparisons.

18.4.2 RMA regression analysis of mean and maximum pressure-speed correlation across the plantar surface

The strength of the pressure/speed relationship for mean and maximum peak pressure are indicated by the correlation coefficient ($r = >0.5$) and are shown in Table 6. This reveals strong ($r = >0.75$) to moderate ($r = >0.5$) support for a linear increase in mean and maximum pressure in 14/15 subjects. The correlation coefficient is measured by the coefficient of determination ($r^2 = >0.5$) in which we find strong ($r^2 = >0.75$) to moderate ($r^2 = >0.5$) support for increasing mean pressure in 12/16 subjects, and in 14/16 subjects for increasing maximum pressure. The significance of the pressure/walking speed relationship is expressed in probability levels ($p = <0.05$). Significant increasing mean pressure was found in 7/16 subjects, and in 8/16 for increasing maximum pressure.

Plotting the SD of average mean and average maximum pressure with speed revealed considerable overlap in average mean and average maximum SD step-to-step. The total range of average mean and average maximum pressure values from the whole plantar surface overlapped across the range of walking speeds (Figure 11a,b).

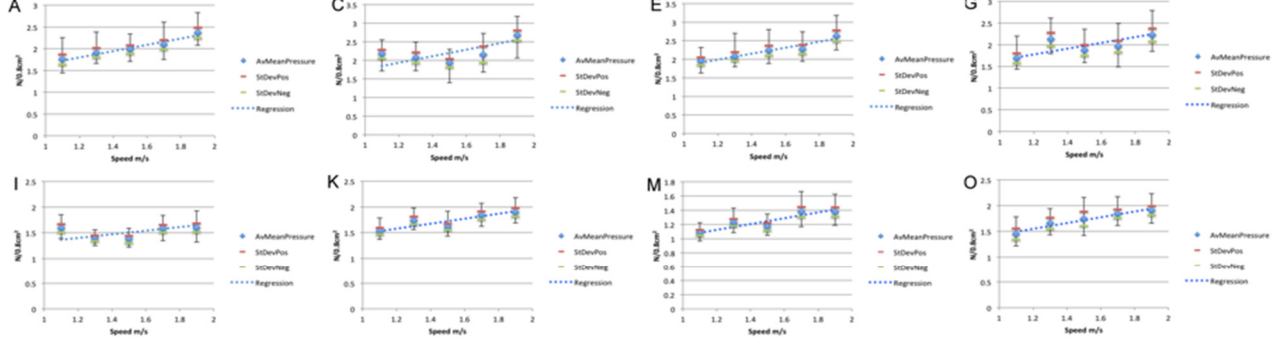
18.4.3 RMA regression of mean and maximum pressure-speed correlation of the midfoot region

The correlation coefficient (r) provides strong to moderate support for decreasing mean and maximum pressure in the pre-defined midfoot region in only 4 subjects (Table 7). There is no support, strong or otherwise, for decreasing mean or maximum pressure with speed from the coefficient of determination (r^2). A statistically significant decrease in mean and maximum pressure with speed was found in only 1/16 subjects ($p = <0.05$). Thus, there are consistently conflicting results reported from pSPM and RMA analyses of discrete variables, justifying the use of these two measures for comparison.

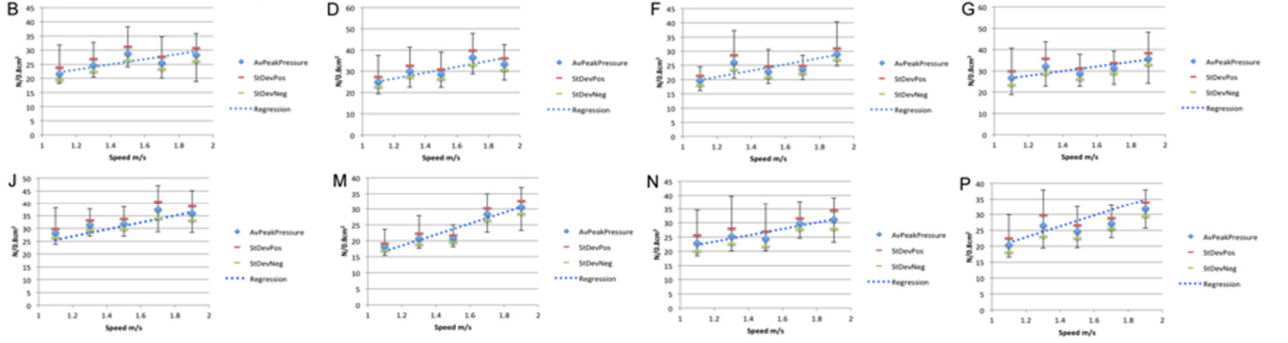
Plotting average mean and average maximum midfoot pressure with speed revealed a large range in midfoot pressure values, with considerable overlap in the SD of average mean and average maximum

pressure step-to-step, such that they overlapped across the entire range of walking speeds (Figure 11c,d).

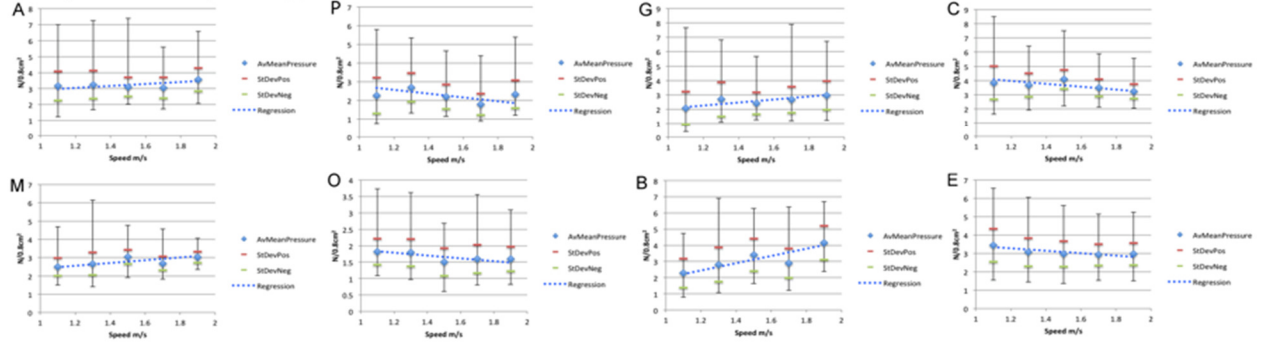
Average mean whole foot pressure (a)



Average maximum whole foot pressure (b)



Average mean midfoot pressure (c)



Average maximum midfoot pressure (d)

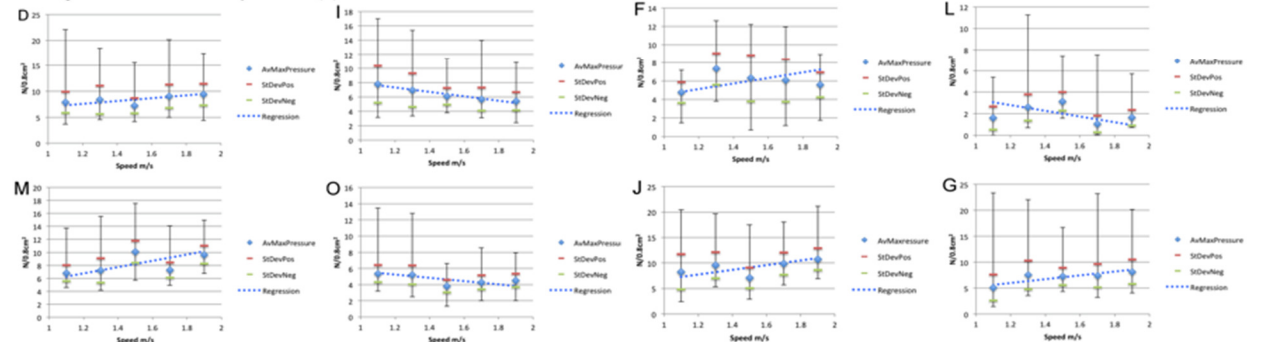


Figure 11

RMA regression analysis reports linear increase in average mean and maximum plantar pressure with speed in all subjects ((a), (b)) and an increase in average mean and maximum midfoot pressure with speed in 7 out of 16 subjects ((c), (d)). The range of average mean and maximum plantar pressure (shown here by the standard deviation) shows large overlap across walking speeds, the plantar surface and the pre-defined midfoot. Subjects' G and M express the highest and lowest MSE respectively, while the other subjects presented were randomly selected due to the highly variable nature of the results.

Table 6

Supporting statistics for changes in mean and maximum plantar pressure with walking speed RMA regression statistics (r , r^2 and p -values) reveal significant increases in mean pressure with speed in 7 subjects (A,E,F,H,M,N,O) and an increase in maximum pressure with speed in 8 subjects (E,H,I,L,M,N,O,P), across the plantar surface.

Subject	Variable	Slope	Intercepts	P-values	r	r^2
A	Mean Pressure	0.723	0.930	0.004	0.974	0.949
	Max Pressure	15.128	1.051	0.910	0.954	0.0117
B	Mean Pressure	0.908	1.319	0.059	0.862	0.7440
	Max Pressure	9.207	12.026	0.124	0.773	0.598
C	Mean Pressure	0.882	0.877	0.272	0.611	0.374
	Max Pressure	17.736	3.308	0.171	0.717	0.515
D	Mean Pressure	1.472	0.972	0.061	0.859	0.739
	Max Pressure	13.916	9.883	0.081	0.830	0.689
E	Mean Pressure	0.814	1.011	0.010	0.956	0.915
	Max Pressure	12.960	16.405	0.009	0.960	0.921
F	Mean Pressure	0.568	0.902	0.0210	0.145	0.815
	Max Pressure	11.102	7.595	0.522	0.723	0.167
G	Mean Pressure	0.663	0.979	0.204	0.682	0.465
	Max Pressure	10.797	14.738	0.120	0.779	0.607
H	Mean Pressure	0.756	1.762	0.008	0.964	0.929
	Max Pressure	15.049	9.085	0.034	0.904	0.818
I	Mean Pressure	0.355	0.976	0.634	0.291	0.084
	Max Pressure	15.889	3.641	0.040	0.894	0.799
J	Mean Pressure	0.3273	1.549	0.252	0.632	0.399
	Max Pressure	13.606	10.498	0.918	0.064	0.004
K	Mean Pressure	0.481	1.000	0.057	0.865	0.749
	Max Pressure	10.086	12.276	0.099	0.805	0.648
L	Mean Pressure	0.719	0.5991	0.065	0.853	0.728
	Max Pressure	15.880	5.561	0.014	0.947	0.896
M	Mean Pressure	0.406	0.637	0.039	0.896	0.803
	Max Pressure	17.209	-2.212	0.014	0.947	0.897
N	Mean Pressure	0.872	1.057	0.017	0.940	0.885
	Max Pressure	11.285	9.785	0.022	0.928	0.862
O	Mean Pressure	0.654	0.873	0.005	0.971	0.942
	Max Pressure	14.345	6.892	0.023	0.926	0.859
P	Mean Pressure	0.589	0.863	0.127	0.770	0.593
	Max Pressure	17.332	1.957	0.015	0.945	0.894

Table 7

Supporting statistics for changes in mean and maximum midfoot pressure with speed RMA

regression statistics (R , R^2 and p -values) reveal significant decrease in mean midfoot

pressure with speed in 1 subject (I) and a decrease in maximum midfoot pressure with speed

in 1 subject (I).

Subject	Variable	Slope	Intercepts	P-values	R	R ²
A	Mean Pressure	0.625	2.294	0.424	0.470	0.221
	Max Pressure	2.447	3.837	0.127	0.770	0.593
B	Mean Pressure	2.238	-0.246	0.063	0.857	0.735
	Max Pressure	7.156	-2.800	0.054	0.870	0.757
C	Mean Pressure	-1.021	5.200	0.209	-0.676	0.457
	Max Pressure	-1.789	10.975	0.231	-0.654	0.427
D	Mean Pressure	0.872	1.542	0.510	0.395	0.156
	Max Pressure	2.744	4.260	0.220	0.665	0.442
E	Mean Pressure	-0.675	4.098	0.093	-0.813	0.662
	Max Pressure	-1.222	11.076	0.525	-0.382	0.146
F	Mean Pressure	0.967	0.643	0.899	0.079	0.006
	Max Pressure	-3.249	11.141	0.966	-0.0263	0.000
G	Mean Pressure	1.053	0.987	0.824	0.829	0.687
	Max Pressure	3.673	1.576	0.097	0.808	0.653
H	Mean Pressure	0.7685	1.756	0.841	0.125	0.015
	Max Pressure	6.274	-0.450	0.545	0.365	0.133
I	Mean Pressure	-0.818	3.253	0.016	-0.942	0.888
	Max Pressure	-3.054	10.963	0.004	-0.975	0.952
J	Mean Pressure	1.487	0.441	0.177	0.711	0.506
	Max Pressure	4.576	2.241	0.304	0.580	0.336
K	Mean Pressure	-0.636	2.645	0.642	-0.284	0.081
	Max Pressure	2.996	1.526	0.910	0.070	0.004
L	Mean Pressure	-0.742	1.906	0.770	-0.181	0.328
	Max Pressure	-2.658	5.997	0.653	-0.275	0.076
M	Mean Pressure	0.765	1.650	0.180	0.708	0.502
	Max Pressure	4.863	0.913	0.300	0.584	0.341
N	Mean Pressure	0.618	1.658	0.536	0.372	0.138
	Max Pressure	3.296	1.469	0.237	0.647	0.418
O	Mean Pressure	-0.436	2.317	0.149	-0.744	0.553
	Max Pressure	-2.036	7.695	0.247	-0.636	0.405
P	Mean Pressure	-1.025	3.797	0.518	-0.387	0.150
	Max Pressure	-3.277	11.284	0.141	-0.753	0.567

18.5 Discussion

This chapter presents a comparative analysis of changes in simple mean and maximum pressure metrics with walking speed by: linear regression, and also, discrete walking speed comparisons from the whole plantar surface, and linear regression using pSPM. The aim was to determine the linearity of the relationship between mean and maximum pressure with a range of walking speeds. As mentioned, the range of speeds in this analysis was determined based on average speeds quantified for young and healthy people (Bohannnon and Andrew, 2011), making these results inapplicable to clinical conditions, or the population as a whole, due to the high variability in human foot and ankle function, and plantar pressure (Bates, et al., 2013a; Venkataraman, et al., 2013).

Firstly, the discrete linear regression walking speed comparison by pSPM (Figure 10) suggests that while a general linear relationship in pressure with walking speed is present, highly variable combinations of increasing and decreasing pressure patterns with walking speed are observed in this sample (Pataky, et al., 2008), and are not very well described by traditional regional boundaries. In various combinations, subjects regularly express decreasing pressure under the proximal lateral forefoot in particular, but also consistently transversally across the MTHs 5-2, supporting a study by Pataky, et al., (2008), who reported decreasing pressure at smaller range of walking speeds supporting a previous study by Rosenbaum, et al., (2004).

Secondly, statistically significant differences between peak and mean pressure were evident in the mid- and forefoot when the most disparate speeds were compared in all subjects when 1.1m/s vs. 1.9m/s, but less than half the subjects (7/16) when 1.1m/s vs. 1.7m/s were compared (Figure 10, see: supplementary material S17.3, S17.4). Both results are discussed and contextualised against previous studies that interpret the functional relationships between foot bone motion, plantar pressure and speed (Pataky, et al., 2008; Caravaggi, et al., 2010, 2016).

For ease of analysis, many studies, including the present contribution, subjectively regionalise the midfoot. However, this has been shown to statistically bias continuous pressure fields, and does not account for relationships between pressure, and anatomy and function (Pataky et al 2008). This premise is in accordance with Figure 7 that reveals unique spatial distributions of increasing and decreasing pressure with walking speed, such that pressure decreases are evident in both transverse and longitudinal directions along the MT complex, and the MTHs. Pressure is shown to decrease across the anatomical distal midfoot (MTs 5-2) and lateral proximal forefoot (MTHs 5-3) in 15/16 subjects supporting previous results (Rosenbaum, et al., 1994; Cavanagh, et al., 1998; Taylor, et al., 2008; Pataky, et al., 2008), and suggesting that perhaps a redefinition of regional pressure descriptors would better describe the habitual pressure patterns expressed in this sample (Figure

7). Increasing pressure under the hallux and phalanges is evident in all subjects to varying spatial degrees. Recently, Barn, et al., (2015) reported variability in the range of dorsiflexion at the ankle joint as a strong predictor of peak plantar pressure across the plantar surface, but a poor predictor of increasing pressure in the hallux or phalanges (Barn, et al., 2015). Within this context, the phalanges and hallux may be specifically tuned for propulsion with reduced relationship to the mechanisms posterior to it. This lends support to the concept that peak pressure is continuous throughout stance phase (Pataky, et al., 2010, 2011).

This is consistent with the findings of Caravaggi, et al., (2010), who showed varying tension in the PA during late swing and stance phase increasing from MTHs 5-1. This suggests a key role of the windlass mechanism (Hicks, 1954) reflected in both pressure patterns and propulsion. The vGRF applied across the dorsiflexing MTPJs, offsets superincumbent body weight step-to-step, by increased stiffening of the PA from pre-stance thereby enhancing late stance phase propulsion (Wolf, et al., 2004). Further, the increased stiffness of the PA during late stance reduces inter-joint motion at the MTPJs prior to heel-strike and reduction increases through to toe-off (Caravaggi, et al., 2010). This extended windlass mechanism might be expected to reduce pressure under the MTHs, while delaying the onset position of propulsive force application until the MTPJs and phalanges –themselves highly propulsive structures (Rolian, et al., 2009). The coordinative complexity of this and other foot

mechanisms driving gait during stance phase are evidenced in Figure 7. High variation in soft tissues provides abundant different combinations of kinematic and kinetic step patterns, expressed at the foot-ground interface. The variable pressure patterns are a reflection of the motor response to external, and internal active and passive forces of the treadmill and the subject. The variable combination of constraints provides a less variable overall set of kinematic and kinetic outcomes step-to-step – essentially providing the most efficient step pattern for each speed trial.

Secondly, linear increases in pressure with speed at the heel are found in at least one subject at each speed comparison, but significance is not consistently expressed in the same subjects across speed comparisons (see: supplementary material Figures S17.1-17.10). This region is most marked likely due to the high decelerative forces produced at heel-strike with increasing speed. Statistically significant decreases with speed only occur in the mid- and forefoot when the most disparate speeds are compared (e.g., 1.1m/s vs.1.7m/s, 1.1m/s vs. 1.9m/s, 1.3m/s vs.1.9m/s) (Figure 10) which supports a previous clinical study using a regionalised approach in patients with diabetic neuropathy (Taylor, et al., 2004). During the two-step-gait initiation protocol, the authors reported increasing pressure in all regions with faster walking speed, but decreasing pressure – as seen in some subjects here (Figure 9), under the lateral midfoot, MTPJ1, and MTPJ3-5. This pattern was observed only at

the most disparate speeds collected in the experiment e.g., 1.4m/s vs. 1.8m/s (Taylor, et al., 2004). The authors suggest that a non-linear response strategy of internal foot motion to velocity may be present in patients with diabetic neuropathy (Taylor, et al., 2004). They also cite the influence of biomechanical differences in the lower limb (e.g., tibial rotation, foot pronation), and differences in the mechanics of normal and fast walking at 1.4m/s and 1.8m/s as further interpretation.

When discrete topological comparisons of walking speed trials were further scrutinised, statistically significant differences were present only between 8 of the 10 subjects. Only 3 subjects report differences between discrete variables at similar speeds (e.g., 1.1m/s vs. 1.3m/s). The subjects with the highest reported discrete topological differences with walking speed were present in 8/10 speed comparisons, but did not exhibit the highest mean or maximum pressure in this sample (subject D). The subject with the highest overall mean and maximum pressure has statistically significant differences only 4/10 times (subject E). Unique combinations of increasing and decreasing pressure with speed is evident at the heel, midfoot, forefoot and phalanges with each speed comparison between subjects (Figure 10, see: supplementary material, Figures S17.1-S17.10). That the subjects with the highest peak and mean pressure only shows statistically significant differences a quarter of the time (4/10), however, the subject with the highest occurrence of differences in discrete comparisons (8/10), reports only average mean and maximum pressure

from the sample here. This could indicate that individual hard tissue morphology and soft tissue tuning variation between individuals may play a role in functional interpretations of pressure.

High levels of step-to-step variation in peak plantar pressure were observed, with considerable overlap in the SD across all walking speeds in this cohort (Figure 11a,b), and are particularly high in the midfoot (Figure 11c,d), supporting previous results (Bates et al. 2013). However, the high levels of variability observed are either unexplained, or unaccounted for in interpretations (Hughes, et al., 1991; Rosenbaum, et al., 1994, Zhu, et al., 1995; Kernozek, et al., 1996; Brown & Mueller, 1998; Drerup, et al., 2001; Burnfield, et al., 2004; Segal, et al., 2004; Taylor, et al., 2004; Warren, et al., 2004; Yang, et al., 2005; Shu, et al., 2010). It is assumed that the high range in variability in midfoot pressure observed here (Figure 11, supplementary material S17.11- S17.15) reflects the wide range of motor control patterns available to plantar soft-tissues (Turvey, 1990) to control the high redundancy in foot motion (Riley and Turvey, 2002; Alexander, 2003; Nester, et al. 2007), and reinforcing the windlass mechanism throughout stance phase (Wolf, et al., 2004). This assumption is supported by the discrete analysis, in that an overall decrease in pressure in the midfoot with walking speed was reported in only a quarter of the cohort (4/16) (Table 6).

That statistically significant differences in the mid- and forefoot occur at only the most disparate speeds (e.g., 1.1m/s vs.1.7m/s, 1.1m/s vs. 1.9m/s, 1.3m/s vs.1.9m/s), could reflect the relatively small incremental increase in walking speeds (0.2m/s), and the reduction in gait variability typically seen in treadmill walking (Dingwell, et al., 2001). In this sample the walking speed range was selected specifically to capture the widest range of walking ability, from slower than average at 1.1m/s, to the walk-run transition at 1.9m/s (Bohannon and Andrew, 2011). A better assessment of changes in pressure parameters with speed in healthy populations would be to compare p-images from an even slower walking speed e.g., 0.5m/s vs. 1.9m/s, where motor control would be potentially more challenged in controlling stability during walking in healthy subjects. Furthermore, treadmill walking has the effect of reducing variability in segment kinematics (Wank, et al., 1998) and the vGRF (White, et al., 1998; and see: Pearce, et al., 1983; Arsenault, 1986), potentially obscuring statistically differences between similar walking speeds that may be present in overground walking (Dingwell, et al., 2001). In addition, a free running, or anti-gravity treadmill may also give a different result, as they act to reduce weight bearing pressure on the lower extremities (Saxena et al. 2011; Patil et al. 2013).

18.6 Conclusions

The results presented in this chapter suggest that while a general linearity in peak pressure with walking speed is established, the traditional boundaries that regionalise sub-sets of the plantar surface, are non-representative of pressure patterns reported here. That two, or potentially three functional distinct clusters do exist is clear: one that acts as a passive ground-impactor and the other for generating propulsion. The former is characterised by two parts, evidenced by increasing pressure in the proximal heel and distal phalanges, acting secondary to the latter, which is defined by decreasing pressure along the MT complex in various combinations, in accordance to the windlass mechanism. This also highlights the need for more work to be established surrounding this relationship in healthy adults, to further understand the causative mechanisms underpinning the variation in plantar pressure with speed. The experimental protocol established for this study of healthy subjects suggests that changes in peak pressure with walking speed in the mid- and fore-foot only reach levels of significance when walking speeds are most different (1.1m/s vs. 1.9m/s). It is assumed that this is a reflection of the highly-tuned motor response strategy for treadmill walking in healthy adults, summed at the foot-ground interface, and expressed as highly variable, but consistently patterned behaviour. Employing stronger measures of variability for stability such as the λ (from trunk kinematics) and compared to peak pressure distribution and magnitude, might

provide causative insights into the role that individual intrinsic structures within the foot play in maintaining stability during walking.

19. Variation in the average MSE value in response to random subsampling of n in plantar pressure

19.1 Abstract

Plantar pressure records reflect the 3D (e.g., time-varying) loading pattern of the foot against the ground, and provide insight into relationships between anatomy, neural control and biomechanical function. However, variance in pressure patterns plays a central role in extrapolating experimental findings to the population level, and importantly, the accuracy of variance estimates is generally dependent on trial n . Recent work from large intra-trial n datasets (i.e. >500 records per subject) demonstrates high levels of inter- and intra-subject variance in peak plantar pressure, suggesting small trial n may introduce inaccuracies that have the potential to sway interpretations of pressure variance. Here the sensitivity of intra-subject MSE to n p-images using pSPM and a random subsampling analysis is reported. The range in MSE becomes exponentially larger as n of subsampled p-images reduced, with near identical results achieved across a range of walking speeds. The number p-images required for the range in MSE of randomly subsampled populations to reach less than 5% of the full dataset values is, 401 p-images collected at 1.3m/s. At low subsample n (8-50), the range in MSE of randomly generated subsamples is 25-50% higher than that of the full dataset MSE of >500 p-images. There is a high probability that small trial n

(e.g., <100 p-images) would capture a relatively low proportion of habitual variance in plantar pressure and not reflect the habitual pressure patterns expressed in a larger dataset.

19.2 Introduction

Gait analyses regularly combine multiple calculators of variance, such as the CV ($cv = sd/m$) (Winter and Yack, 1987; Cavanagh, et al., 1998; Owings, et al., 2003; Heiderscheit, 2000; Brach, et al., 2008, Hamill, et al., 1999; 2000; Li, et al., 2005; Wilson, et al., 2008), the MSE (Clancy, 1998; Oriwol and Maiwald, 2011; Wagner, et al., 2012), and various ANOVA measures (Kang and Dingwell, 2008; Crenshaw, et al., 2006; Beauchet, et al., 2009) to better understand changes in locomotor behaviour over time, and between populations. These calculators reflect aspects of variance that describe skill acquisition and motor learning in children and athletes (Newell, et al., 1986; Handford, et al., 1997), and the functional role and, decline of stability, in various types of gait between populations (Cavanagh, et al., 1998; Beauchet, et al., 2005).

The reliability of the reported measures however, are particularly sensitive to individual trial n . Various studies report improvements in the reliability and accuracy of variability and stability measures as individual stride n increased (Dingwell, et al., 2001; Owings and Grabiner, 2003; Hollman, et al., 2010; van Schooten, et al., 2013; Riva, et al., 2014).

However, for some populations, walking for more than >100 strides is not achievable due to pain and discomfort brought on by walking, and as a consequence, clinical trials can present low individual trial n .

Consequently, it is important that the sensitivity of variability measures to individual trial n is better understood.

This is of particular relevance to analyses of peak plantar pressure, which play a central and practical role in clinic; e.g., predicting factors that contribute to abnormalities in high-risk populations (Barn et al., 2015), reducing the advancement of pre-existing conditions (e.g. Frykberg, et al., 1998; Pham, et al., 2000; Boulton, et al., 2004), and identifying therapeutic interventions (Owings, et al., 2008; Bus, et al., 2011; Paton, et al., 2011). However, valid interpretations p-images, rest on the assumption that either a single p-image, or sample of p-images, reliably characterises the habitual foot mechanics in the individual, or group under study, relative to unique implementation procedures. A previous study of variability (MSE, CV) in plantar pressure could not detect differences between diagnostic populations of diabetic, and diabetic neuropathic cohorts, however the individual trial n was low (50 mid-gate) and the plantar surface regionalised (Cavanagh, et al., 1998), and called specifically for validation by larger individual trial n of continuous steps. While this study is not relevant to clinical trials, it provides initial insights into the sensitivity of MSE to individual sample n as called for by Cavanagh and colleagues (1998). Recent studies of peak plantar pressure by MSE from non-clinical

trials with large individual trial n (>500 records per subject), reported high levels of inter- (i.e., between individuals) and intra-subject (i.e. step-to-step) variance in peak midfoot, and whole plantar surface pressure in healthy subjects (Bates, et al., 2013b). These support previous results from a clinical study of patients with diabetic neuropathy, reporting broadly similar variability in peak pressure step-to-step across the diagnostic groups in the study (Cavanagh, et al., 1998). To further delineate features of plantar pressure analyses that are effective for future exploration of the measurement in research, an assessment of the sensitivity of the MSE to individual trial n is necessary.

The aim of this study is to compare the range of MSE of randomly generated subsamples of individual trial n ranging between 5-400 p-images, to the range in MSE of the total individual trial n of >500 p-images, to quantify the average by which the MSE varies as individual sample n increases or decreases.

19.3 Materials and methods

19.3.1 Data collection

The dataset described in section 14.1 and 14.2 is used here for this subsampling analysis because of the size and range of walking speeds it encompasses (i.e. >500 records per subject per speed from 1.1-1.9m/s).

19.3.2 Data processing

Pressure values corresponding to the maximum pressure recorded in each cell, during each subject's footfalls were extracted using a custom-written C program. This yielded a *total* individual trial n per subject ranging from $n = 520-721$ p-images per speed, with shorter individuals taking more steps (producing more records) during the data collection time (McClymont, et al., 2016). P-images from each subject's total individual n were registered to each other, followed by separate registration of the p-images contained in each separate individual speed trial, using a recently described algorithm (Pataky and Goulermas, 2008), that minimises the mean square error (MSE) between neighbouring pixel vectors during registration both within individual p-image, and between p-images. This process facilitates statistically robust comparisons to be made between pixels and conditions (Friston, et al., 1995; Pataky and Goulermas, 2008; Pataky, et al., 2008).

19.3.3 Data analysis

The broadly consistent foot contact shape and geometry shared between subjects allows the spatial registration and direct comparison of each step taken in the trials. To investigate the sensitivity of the range of MSE to individual trial n , the mean of each individual speed trial, and the mean of the total individual trials were calculated. The MSE was calculated from each pixel, in each p -image in all individual speed trials according to:

$$\text{MSE} = 1/N \sum (I_{0k} - I_{1k})^2$$

where N is the total number of non-zero pixels in the mean image; I_0 is the mean of the subject's overall sample and I_1 is an individual pedobarographic record. The MSE of each pixel was then summed to produce a total MSE value for each individual p-image about the subject's overall mean p-image.

To quantify to quantify the average by which the MSE varies with individual trial n , we conducted a random subsampling analysis for each speed from each subject. Smaller subsamples of p-images were extracted randomly from each subject's total individual trial n , at subsets of $n = 5, 25, 50, 100, 200, 300, 400$ and 500 in a Monte-Carlo simulation. This was performed 1000 times at each speed of n subsets for each subject. The range in MSE given by the 1000 randomly generated samples for each subset was then calculated with respect to the subject's total individual trail MSE at that speed, enabling quantitative comparison of the sensitivity of intra-subject MSE to individual trial n . Only the results from 1.3ms are presented here as results are consistent across all speeds (supplementary material S16. 1-S16. 8) tested in this sample, further 1.3ms represents average walking speed for healthy adults, as evidenced by experimental studies of pedestrian walking (Himann, et al., 1988; Öberg et al., 1993).

19.4 Results

Figure 12 (Table 8) shows the results of the Monte Carlo random subsampling analysis for the sensitivity of the range of MSE to individual trial n at a speed of 1.3ms. Individual trial n has a clear effect on the range in MSE with values decreasing exponentially as individual trial n increases (Figure 12, Table 8). The minimum number of p-images required for the range in MSE to fall within 5% of the total individual trial n range in MSE, is $n = 401$ at 1.3ms (Figure 13, Table 9). At smaller subsample sizes (i.e. $n = <10$) the range in MSE values exceeds 75% of the total individual trial n MSE range, from which the subsample was randomly selected (Figures 12, 13). Results are consistent to within ± 70 p-images across the walking speed trials in this analysis (1.1ms, 1.3ms, 1.7ms, 1.9ms) and are provided in the supplementary material (see: supplementary material, Figures S18.1-S18.8). Figure 14 exhibits the high level of step-to-step variability in peak pressure in the first 12 p-images collected during the individual walking speed trial of 1.3ms from the subjects with the highest and lowest MSE (Table 4).

Table 8

N p-images (n) required to reach within 75%, 50%, 25%, 10% and 5% range of the total sample range MSE at each speed collected.

Normalised MSE	(n) = 75%	(n) = 50%	(n) = 25%	(n) = 75%	(n) = 95%
1.1ms	9.21 (9)	16.94 (17)	46.26 (46)	187.46 (187)	330.9 (331)
1.3ms	8.82 (9)	15.81 (16)	46.55 (47)	222.95 (223)	401.35 (401)
1.5ms	8.88 (9)	16.31 (16)	49.95 (50)	199.01 (199)	348.88 (349)
1.7ms	8.42 (9)	14.94 (15)	47.92 (48)	198.79 (199)	350.1 (350)
1.9ms	9.13 (9)	16.53 (17)	46.69 (47)	230.31 (230)	417.16 (417)

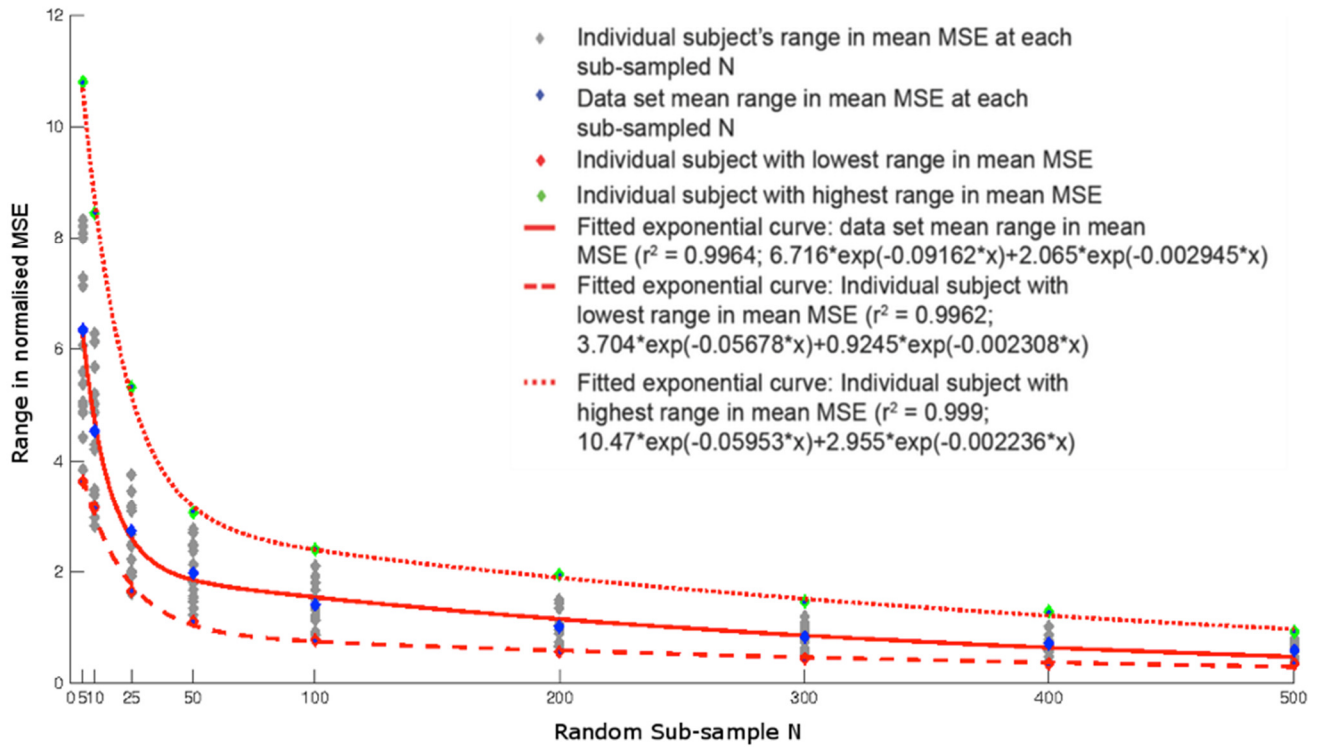


Figure 12

The relationship between individual trial n and the sensitivity of the MSE at randomly generated subsamples ($n = 5, 10, 25, 50, 100, 200, 300, 400, 500$), re-generated 1000 times per sub-sample at 1.3ms. Exponential curves describe this relationship well in all subjects.

This relationship is observed here plotting the combined mean of all 16 subjects (solid curve), and the individual 1.3ms trial mean of the subjects with the highest (subject G, dotted curve) and lowest (subject M, dashed curve) overall MSE.

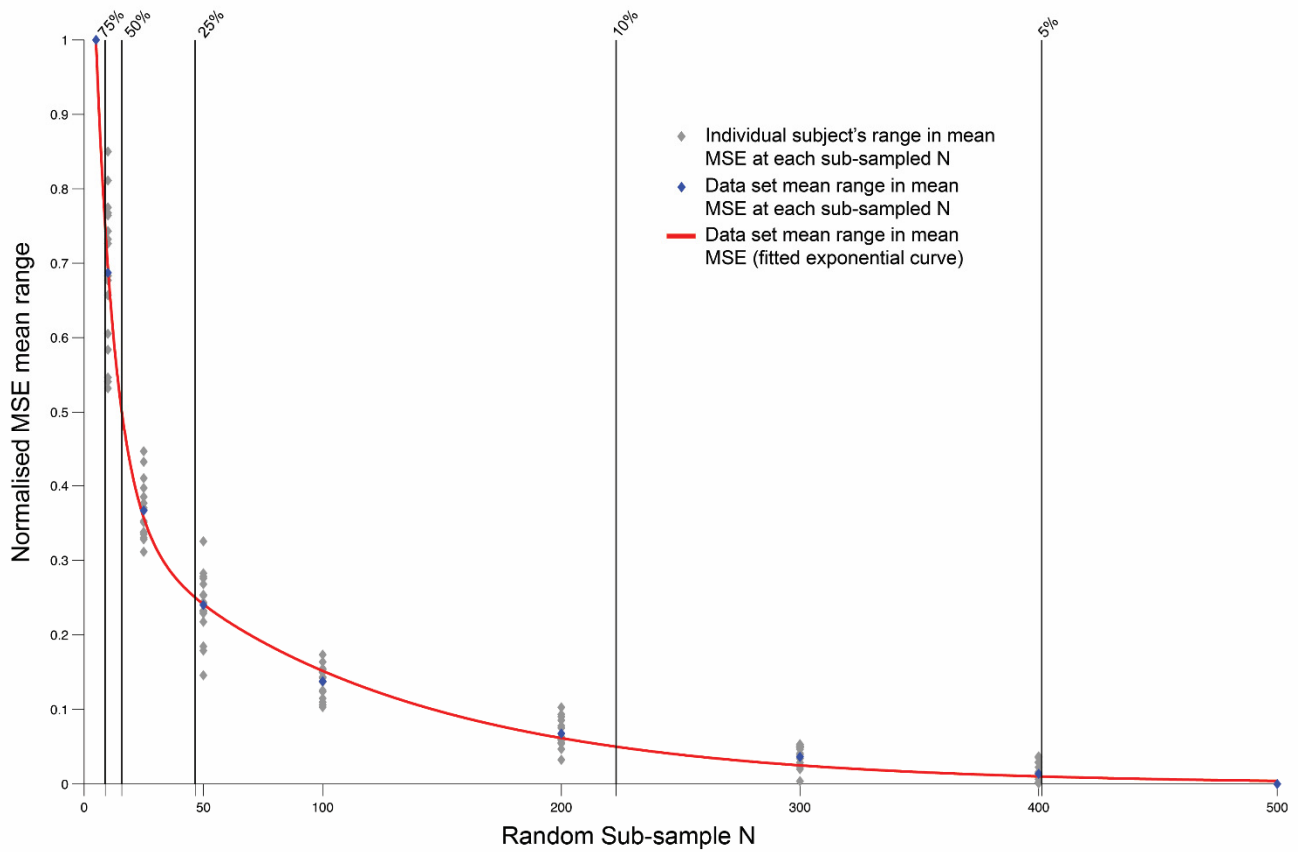


Figure 13

The relationship between randomly generated subsample n (randomly generated 1000 times), and reports the n necessary to reach within 5%, 10%, 25%, 50% and 75% of the range in MSE at each subsample (vertical lines). The range in MSE is plotted as a percentage of the MSE value of the individual walking speed trial n , at 1.3ms. When sample size is $n = >400$ pressure records, then the range in MSE (given by the 1000 randomly generated subsamples) is less than 5% of the individual walking speed trial MSE for each subject. The observed range in MSE at smaller individual trial $n = <25$ is only within 50% than the total individual trial MSE observed for each subject.

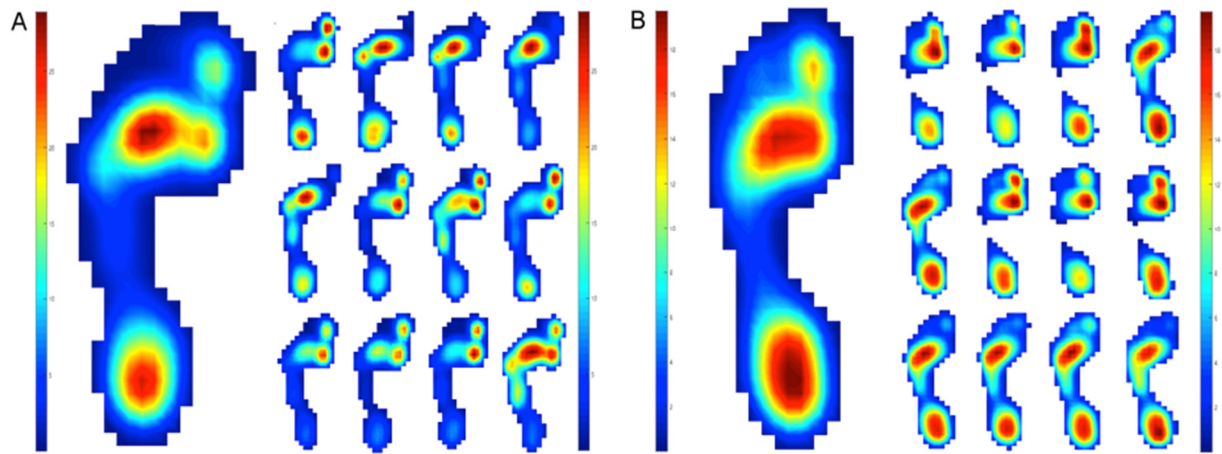


Figure 14

Mean peak plantar images (left, large p-image) and the peak plantar pressure records from the first 12 consecutive steps (right, smaller p-image) from the subjects with the highest (A, subject G) and lowest (B, subject M) MSE to illustrate high levels of step-to-step variability in pressure distribution.

Table 9

Exponential equations describing the relationship between subsamples of individual trial n and the range of MSE from 1000 randomly generated subsamples.

Subject	Exponential equation	r^2
1.1ms		
Least variable	$f(x) = 2.284 \cdot \exp(-0.054 \cdot x) + 0.64 \cdot \exp(-0.0018 \cdot x)$	0.97
Mean	$f(x) = 5.66 \cdot \exp(-0.084 \cdot x) + 1.88 \cdot \exp(-0.003 \cdot x)$	0.96
Most variable	$f(x) = 12.66 \cdot \exp(-0.08 \cdot x) + 2.5 \cdot \exp(-0.002 \cdot x)$	0.93
1.3ms		
Least variable	$f(x) = 3.70 \cdot \exp(-0.056 \cdot x) + 0.92 \cdot \exp(-0.002 \cdot x)$	0.97
Mean	$f(x) = 6.71 \cdot \exp(-0.09 \cdot x) + 2.06 \cdot \exp(-0.002 \cdot x)$	0.95
Most variable	$f(x) = 10.47 \cdot \exp(-0.0595 \cdot x) + 2.955 \cdot \exp(-0.002 \cdot x)$	0.96
1.5ms		
Least variable	$f(x) = 3.465 \cdot \exp(-0.16 \cdot x) + 0.76 \cdot \exp(-0.003 \cdot x)$	0.93
Mean	$f(x) = 5.195 \cdot \exp(-0.08164 \cdot x) + 1.642 \cdot \exp(-0.002932 \cdot x)$	0.96
Most variable	$f(x) = 14.15 \cdot \exp(-0.1665 \cdot x) + 3.389 \cdot \exp(-0.003939 \cdot x)$	0.96
1.7ms		
Least variable	$f(x) = 3.318 \cdot \exp(-0.0551 \cdot x) + 1.085 \cdot \exp(-0.0023 \cdot x)$	0.98
Mean	$f(x) = 7.56 \cdot \exp(-0.1257 \cdot x) + 2.104 \cdot \exp(-0.003532 \cdot x)$	0.95
Most variable	$f(x) = 57.95 \cdot \exp(-0.2843 \cdot x) + 5.896 \cdot \exp(-0.004846 \cdot x)$	0.90
1.9ms		
Least variable	$f(x) = 2.279 \cdot \exp(-0.07063 \cdot x) + 0.7358 \cdot \exp(-0.002994 \cdot x)$	0.97
Mean	$f(x) = 5.566 \cdot \exp(-0.08938 \cdot x) + 1.734 \cdot \exp(-0.002981 \cdot x)$	0.95
Most variable	$f(x) = 8.125 \cdot \exp(-0.1242 \cdot x) + 3.476 \cdot \exp(-0.003983 \cdot x)$	0.92

19.5 Discussion

Herein, the aim was to quantify how the average MSE of peak pressure responds to changes in individual trial n . The magnitude of peak pressure variability is expected (Arts and Bus 2011), and proven to be highly variable when calculated both within, and between individuals (Figure 14) (Cavanagh, et al., 1998; Pataky, et al., 2011; Bates, et al., 2013b; Caravaggi, et al. 2016; McClymont, et al. 2016). For example, at a walking speed of 1.3m/s, and an individual trial $n = 10$, subjects with the highest (dotted curve) and lowest MSE (dashed curve), reported 10.3 and 2.2 respectively (Figure 12). When individual trial $n = 400$, the MSE

reduced to 1.5 and 0.4 respectively, to within 5% of the total individual trial $n = >500$ (Figure 13).

The results reported elucidate the sensitivity of MSE in peak plantar pressure at the pixel-level. In general, $n = >400$ strides is much larger than the n conventionally advocated in clinical plantar pressure analyses (e.g., 3-12 p-images) (Kernozek, et al., 1996; Arts and Bus, 2011). Long bouts of walking can lead to patient pain and discomfort, however a compromise between the reliability of the measure, and experimental limitations must be established, if variability measures in peak plantar pressure are to accurately quantify pressure behaviour. By assumption, it could theoretically be suggested that an individual trial $n = 190$ continuous steps (approximately 2 minutes of walking at 1.1m/s, see: supplementary material, Figure S18.5) would more reliably represent the variability in peak plantar pressure than the suggested 8-12 strides (Arts and Bus, 2011).

The potential for sub-optimal interpretations resulting from small individual trial n can be illustrated by visualizing the range in variability step-to-step from just a small number of peak plantar pressure records collected here (Figure 14). Figure 14 shows the first 12 steps at 1.3m/s taken by the subjects with the highest (subject G) and lowest (subject M) MSE (Table 4). The overall pressure distribution and the position of peak pressure step-to-step is highly variable across the plantar surface

regardless of the magnitude of difference in MSE, and very few of these records qualitatively resemble the large, mean pressure image on the left of each subject (Figure 14). Furthermore, subjects in this study did not note large variance in midfoot pressure reported in some healthy subjects in a recent study (Bates, et al., 2013a) where midfoot pressure varied from minimum to maximum step-to-step, across the whole plantar surface in some individuals (Bates, et al., 2013a). Presumably subjects exhibiting such extreme ranges in midfoot pressure would show even more variation over the plantar surface than those analysed herein.

Technological advances in data collection (e.g. instrumented treadmills) and analysis (e.g. automated image analysis algorithms and pixel level statistical comparisons) are making interrogations of very large biomechanical datasets increasingly feasible (Pataky, et al., 2011). These advances are important given the revelation of seemingly high levels of step-to-step variation in peak plantar pressure in recent analyses of larger than normal individual trial n (Bates, et al., 2013a; McClymont, et al., 2016). Previous work on other gait parameters has shown that variability is reduced by treadmill effects, shown to be associated with shorter stride lengths, increased cadence (Pearce, et al., 1983; Arsenault, 1986), changes in segment kinematics and the trajectory of the vGRF (Wank, et al., 1998); White, et al., 1998), significantly affecting local stability during locomotion when compared to overground walking (Dingwell, et al., 2001). Therefore, the specific quantitative findings reported here may not apply to non-

treadmill walking, although it is likely that qualitative results identified here; that is, exponential increases in MSE range as trial n decreases (Figures 4-5) will occur, signifying an increasing likelihood that the sampled data will poorly reflect the central tendency and variation of an individual's habitual peak plantar pressure. The effect that long distance walking, uneven terrain and slope have on pressure parameters are currently under study (Winder, et al., 2014; Allen, et al., 2015). The cohort studied here is composed of entirely healthy individuals. Further work should explore changes in MSE range at different trial n in different age and diseased cohorts to extend these findings to clinical analyses of plantar pressure.

19.6 Conclusions

This chapter quantified the average by which the MSE varies as individual sample n increases or decreases in plantar pressure analyses by pSPM. The results support existing evidence that relatively large individual trial n is required to accurately and reliably interpret the habitual nature of kinematic and kinetic gait parameters. These results demonstrate that the individual trial n typically collected in plantar pressure studies in the literature ($n = 10-50$ p -images) produces MSE ranges that are more than 50% higher than from when sampled from a larger total individual n of >500 . At $n = <10$ records this increases to more than 75%, indicating a high probability that such a small individual trial n

would not reflect either the range of variation, or the habitual mean pressure that would be represented by a larger dataset of more than $n = 500$. These results suggest care should be taken when drawing conclusions regarding the nature and variability in peak plantar pressure from short walking trials.

20. Variability and plasticity in hominins

20.1 Abstract

The evolution of hominin locomotion is interpreted through a combination of functional morphology, ecology and biomechanical principles. However, the high intra- and inter-species variability present in the fossil record, and in the biomechanical behaviour in analogous living primate species, remain understudied. In agreement with some previous suggestions, it is here proposed that a full understanding of the variation in dynamic behaviour in analogous species would strengthen locomotor interpretations from the fossil record. Variability is normal and functional in all biological systems, and is fundamental to the adaptive success of populations. Here it is suggested that current methods should be expanded to include local dynamic stability in living analogous primates, with the goal of establishing a more detailed insight into the diversity of locomotor modes within and between populations, and taxa in line with the extended evolutionary synthesis. A standardised measure of stability collected from tri-axial inertial sensors and 3D video photogrammetry (most practically in rehabilitation centres), would expand the current understanding of primate motor control and how it achieves stable, adaptable locomotion during a range of behaviours and across ontogeny. Understanding the relationship between the unique morphological features of living primates, and the range of locomotor behaviours they display, would help refine locomotor interpretations from functional

morphology, to further elucidate the similarities and diversity present in dynamic locomotor evolution. As a use-case scenario, a statistical analysis of the step-to-step topological variability reveals high stride-to-stride topological variability in the most complete fossil footprint trail, Laetoli G-I, when footprint depth is taken as an analogue for pressure. This agrees with the expectations of dynamical systems theory whereby locomotion is characterised by high intra-subject variability step-to-step. We end by contextualising the paper within the extended evolutionary synthesis (EES) by arguing that locomotor plasticity is a key selective target in hominin evolution.

20.2 Introduction

The preceding chapters 17-20 have reported high intra-subject variability in peak pressure in a small sample of healthy humans. It is assumed here that as in all biological systems, high variability in peak pressure is one of the characteristic states influencing the magnitude and spatial distribution of peak pressure, as the foot interacts directly with the (treadmill) environment (Bernstein, 1967). Pressure variability is universally low in this sample of volunteers, and isolated under the MTH5 and MTH1, showing no relationship to speed (chapter 17). These two regions also express decreasing (MTH5), and increasing (MTH1) pressure in response to different walking speeds in this sample of subjects, however the subject with the highest overall MSE (chapter 18, Table 4)

had the least occurrence of statistically significant differences in the sample. This suggests that changes in peak pressure with speed are not correlated to variability in peak pressure under the conditions in these experiments. It is assumed under dynamical systems theory, that combinations of increasing and decreasing pressure with walking speed are representative of the derived human condition, however this condition is highly variable (Lundgren, et al., 2007; Nester, et al., 2007a; Bates, et al., 2013b; Venkataraman, et al., 2014a,b), due to combinations of internal and external constraints, and the highly diverse range of environments that humans have exploited worldwide. This chapter contextualises these results within the context of the evolution of the human foot, building a framework to specifically analyse, contextualise and interpret variability in hominin evolution.

In mammalian locomotor evolution, adaptations are a product of dynamic interaction with an environment. Ultimately, the morphology of bones reflects habitual locomotor behaviour within the ecological context of its lifetime (Bock, 1965; 1994; Jungers and Minns, 1979; Ruff and Runestad, 1992; Trinkaus and Ruff, 1999; MacLatchy, et al., 2000; Madar, et al., 2002; Ruff, 2002; Ruff, et al., 2006; Handford, et al., 2003). This is the domain of the relatively new field of ecomorphology, that explains the covariation of ecology and morphology (Winkler, 1988). As observed by Bock (1994), robust interpretations of evolutionary adaptations should be “nomological” i.e., regardless of system structure or composition,

underlying phenomena should be explained by similar abstract principles. Specifically, the natural laws of physics underlie a system's capacity to maintain stability during dynamic movement. Thus, natural selection drives adaptations of hard and soft tissue configurations to enhance performance relative to the environment, and each may be studied and distinguished between species (Laland, et al., 2015). This is one of the core assumptions of the EES (Mayr, et al., 1998) termed "reciprocal causation", whereby "organisms shape, and are shaped" equally (*p.* 2, Laland, et al., 2015) by selective and developmental environments. Thus, developmental and niche diversification works *with* natural selection in determining the rate and direction of adaptations (Laland, et al., 2015). In modern biomechanics, the dynamic movement described here are quantified and interpreted by dynamical systems theory (Bernstein, 1967; Newell, 1986; Riley and Turvey, 2002; Latash, 2000).

Foot bones are of particular interest to human locomotor evolution (reviewed e.g., in Klenerman, et al., 2006; D'Août and Aerts, 2008; Sobczak, et al., 2008; Vereecke, et al., 2008) as each interaction with the substrate is achieved by unique configurations of postural and dynamic patterns. Locomotion is characterised by variability and regarded as functional (Arutyunyan, et al., 1968; Davids, et al., 2003); there is intra-individual variability, and equally inter-population variability in morphology and behaviour. Primates are typically large-bodied and predominantly arboreal, thus we argue that ensuring stability and fall-avoidance during

locomotion can be assumed (as it is proven in humans (Calandre, et al., 2005; Lockhart and Liu, 2008)), to be a requirement for reproductive success. A stable gait is simply defined as one that during which the subject does not fall over despite perturbations (Dingwell, et al., 2001; Bruijn, et al., 2013), and is a key parameter to consider in studies of locomotion.

It would appear logical that a similar interpretative nomological framework should be applied in palaeoanthropology to understand the evolution of locomotion in hominins. Such a framework however cannot often directly benefit locomotor interpretations due to small (e.g., $n = 1$), and the fragmentary, incomplete and static nature of the fossil record. There is *some* potential however to interpret performance variation from fossil footprint trails, at least retrospectively. For example, footprints analysed from the Laetoli G-1 (3.66MA presumed *Australopithecus afarensis*) and Ileret (1.5MY presumed *Homo erectus*) fossil trails have been analysed to predict the stride length, foot shape and speed of the trackmaker (Alexander, 1984; Reynolds, 1987; Raichlen, et al., 2008). Further, spatio-temporal characteristics of the same trail have been used as an analogy to predict energetic costs in *Au. afarensis* (Al-333-1) (Kramer and Eck, 2000; Sellers, et al., 2005). Such interpretations are strengthened by analogy to living primates, for example to clarify species boundaries in hominin evolution (Wood and Boyle, 2016). There is still debate however regarding the significance of the taxonomic and

morphological variability in the fossil record (Wood and Boyle, 2016), and a call for broader understanding of the variability in behaviour of living analogous primates (Crompton, et al., 1998; Alexander, 2003; D'Août, et al., 2004; Carlson, et al., 2011). Here, we suggest that a contextualisation of stability, calculated by the λ and supported by an assessment of the variation in stride interval (SI) parameters in dynamic primate behaviour and morphology, and tested against empirical observations, would extend our understanding of the range of variability in morpho-functional relationships, and provide a deeper understanding of stable locomotor behaviour in analogous primates. Such a multi-disciplinary framework could act to more accurately identify hominin species boundaries, and also better understand locomotor evolution in hominins.

Thus, in this paper: a brief description of dynamical systems theory (section 19.3), with specific reference to the intra-variability present and functional in dynamic systems (section 19.3.1), followed by a discussion of high functional redundancy achieved by high degrees of freedom in the foot (section 19.4), with special reference to the variability, and the similarities and differences in foot mechanics in primates (section 19.4.1). Considering the broadly similar locomotor pattern amongst primates, a framework that combines dynamical systems theory, functional morphology and ecomorphology – hereinafter referred to as '*the variability framework*' is suggested to extend, and strengthen interpretations of hominin locomotor evolution. To build the framework, a

statistical comparative assessment of the topological differences in footprint depth from 11 fossil footprints from Laetoli (presumed *Au. afarensis*), Ileret (East African *H. erectus*), Walvis Bay (Holocene *Homo sapiens*) and experimental studies of modern humans (Modern *Homo sapiens sapiens*) are presented (section 19.5), with discussion focussed on the high redundancy in the foot and substrate effects (section 19.5.1). The interpretation is contextualised by the pre-existing literature assessing variation and variability from the fossil record (section 19.5.2). The variability framework is then presented (section 19.6), suggesting the quantification of local orbital stability by λ , and, and stride-to-stride variability in SI parameters as a complementary measure to λ , ideally collected in rehabilitation centres, alongside the use of CV in functional morphology (section 19.6.1-19.6.4). Further, it is suggested that these data are correlated with the variation in locomotor behaviour and mode in free-ranging extant primates. This is by no means a trivial task, thus we suggest technology and analyses that are specifically selected to simplify and counter the difficulties associated with the collection of biomechanical data from primates, in wild type settings. Finally, we discuss the potential of this framework in providing evidence for selection for locomotor plasticity in hominins specifically (section 19.7).

20.3 Dynamical systems theory

Dynamical systems theory provides a comprehensive, multidisciplinary approach that describes the behaviour of complex dynamical systems, by recounting movement patterns over different timescales (Williams, et al., 1999; Davids, et al., 2003). Its development in biomechanics and functional analysis was rooted in the science of complex systems, the field of analysis that describes the change in behaviour of systems over time (Riley and Turvey, 2002). In primate locomotion, the natural laws of physics, mathematics and biology define the interaction of parts to produce successful movement, by exploiting available motor options (Bar-Yam, 2002; Chapouthier, 2009). There are four primary measures of stability that are core to dynamical systems theory: λ ; CV; the maximum Floquet multiplier (mMF), and long-range correlations. Here, we discuss variability measured by the λ and CV; as a calculator of stability during locomotion in the former, and in SI variability in the latter. Readers are directed to Brujin, et al., (2013) for an excellent tutorial by which to calculate and analyse the stability and variability measures described here.

20.3.1 Intra-variability in dynamic systems

Vertebrate gait is characterised by rhythmic and variable fluctuations in SI parameters that functionally stimulate stability during

locomotion (Grillner, 1985; Arutyunyan, et al., 1968; Hausdorff, 1996, 1997; Dingwell, et al., 2001; Jordan, et al., 2007) e.g., in humans, the classic rhythmic alternating activity is the inverted pendulum. Bernstein (1967), described movement as “repetition without repetition”, i.e., each movement task (e.g., step) is driven by a unique set of neural and motor patterns, temporarily assembled to produce a task outcome (Latash, et al. 2002). For example, CV of step length and width change with time and relative to external and internal constraints in all animal locomotion, driving the highly diverse variety of dynamic movement behaviours amongst them (Bernstein, 1967; Alexander, 1991; Bock, 1994). The standard CV equation ($CV = \frac{SD}{m}$), however, is not a measure of stability in a moving system (Dingwell, et al., 2001; Bruijn, et al., 2014; van Emmerik, et al., 2016). The CV reflects the distribution, or range of a parameter about the mean, but does not directly infer levels of stability, and is thus not presented here in a dynamic context. Differences in the CV of step kinematics are relatively small e.g., only a few percent increase or decrease in parameter change will occur, signifying the finely tuned nature of motor control mechanisms that regulate gait patterns (Hausdorff, 1997; Alexander, 2003). Subtle differences in the magnitude of variability are task and environment dependent, affected by ageing, neurological and pathological status and have a rich history in locomotor biomechanics (Gabell and Nayak, 1984; Hausdorff, et al., 1997; Terrier and Schutz, 2003; Jordan, et al., 2007; Vaillancourt, et al., 2003).

In humans walking under laboratory conditions, fluctuations in stride length (SL) and stride frequency (SF) facilitate stable walking. Variability in fluctuations is functional, and controlled by long-range correlations exhibiting fractal-like neurophysiological behaviour (Bak and Creutz, 1994; West and Griffin, 1999; Griffin, et al., 2000; Goldberger, et al., 2002). These latter are defined by power-law correlations whereby parameters increase exponentially in response to each other, and “memory” affects the pattern of fluctuations in SI at any moment, such that SI variations are a direct product of previous SI variations from multi-varying time scales (Hausdorff, 1996). Further, Hausdorff, et al., (1997) reported that when subjects walked voluntarily for 5 minutes, long-range correlations were reported under power-decay-law for over 1000 strides at three voluntary walking speeds. When walking to a metronome, variations in SI were not correlated, i.e., non-fractal, suggesting variation in SI is a functional and omnipresent aspect of motor control of walking (Hausdorff, 1997). Previous work suggests that this mechanism should be developed in primates (Grillner, 1985), but methods or analysis to evaluate the potential mechanisms underlying fractal-behaviour in primate locomotion are not presented as part of this framework.

Local stability, assessed by λ , quantifies the average logarithmic rate of divergence of a system in response to perturbations (Rosenstein et al. 1993; Dingwell and Cusumano 2000). The λ reflects real time motor

control response to small changes in initial conditions – i.e., a perturbation. A positive λ indicates divergence of two initially neighbouring trajectories, rendering the system unstable (Rosenstein, et al., 1993; Dingwell, et al., 2001; Bruijn, et al., 2013). For robust inference of stability, the time dependent position of a point i.e., CoM in ambient space, the starting positional state space must be the same, and the same number of steps must be compared across trials (Bruijn, et al., 2013). The state space refers to the same position, velocity or acceleration of the point; here the CoM can be defined from proximal and distal dorsal spine segments.

In dynamical systems, self-organising patterns are coordinated by the interaction of the vestibular and sensorimotor systems (Davids, et al., 2003). Interacting system parts are coordinated relative to internal (genetic, injury, morphology) and external (environmental) constraints (Kugler and Tuvrey, 1987), guiding the system through momentary adaptive states step-to-step (Davids, et al., 2003). Neuromuscular control patterns are formed to move joint centres in, and out, of “state-spaces”, which are momentarily, and instantaneously, stable, and uniquely assembled to maintain stability (Kelso and Ding, 2003). Feedback loops coordinate order parameters and control parameters to organise the structure (order) and pattern (control) that defines the state space. For example, order parameters structure the influx of kinetic energy into the limbs, and control parameters provide the pattern to increase limb

oscillation, enabling the switch from walking to running (Haken and Wunderlin, 1990).

20.4 Redundant degrees of freedom

The adaptive complexity described here requires that biomechanical degrees of freedom at joints exceed the minimum number required to complete a complex motor task, facilitating “greater economy of movement” (Bernstein, 1967). Given the high frequency of foot-ground interactions, and interactions with variable substrates during orthograde locomotion there are many degrees of freedom in the foot (Davids, et al., 2003). The 26 bones, 33 joints, and over 100 soft tissue components in the foot follow this expectation, possessing as many as a theoretical 180 degrees of freedom (*pers comm*: Alberto Minetti).

Through coordinative patterned behaviour thus dynamic systems are able to engage with, and overcome, constraints by exploiting high levels of functional redundancy (Bernstein, 1967), or abundance (Latash, 2000; 2001). Dynamical systems control excessive redundancy by assembling individual ‘coordinative structures’ step-to-step (Turvey, 1990), temporarily constructing rigid couplings that cross multiple joint-components in the foot. A recent contribution attempted to model the described complex internal foot behaviour experimentally in a subject specific, 26-segment foot model whereby soft-tissue constraints fluctuated to coordinated the degrees of freedom available to the step (Oosterwall, et

al., 2011), but dynamical systems equations were not employed in this model. Coordinative structures exploit the inter-connectedness of the moving parts of the system in a unique, temporary and flexible way (Kay, 1988). The effectiveness of coordinative structures is rooted in the mechanical tuning of the structure (Turvey, 1990; Carrier, 1994; Wolf, et al., 2008). An important aspect of this feature is that if one motor pattern contains an error, the other parts of the structure will automatically vary their contribution to minimise the impact of the error to maintain a stable movement outcome (Latash, 2002).

20.4.1 Variability in the foot

A plantar pressure record reflects the individual vertical component of the vGRF against the plantar surface (Oosterwall, et al., 2011). The centre of pressure is the summation of muscular forces applied through the body to the ground, and is a direct reflection of the path of the CoM over the base of support (Winter, 1995). Pragmatically, pressure records could be described as a snapshot of the final motor pattern selected for the step concerned. Recently Caravaggi, et al. (2016) demonstrated a statistical link between internal foot bone motion and plantar pressure. This is evidenced by a high range of inter-tarsal bone motion in individuals, supporting evidence of high degrees of freedom in the foot (for human range see: Nester, et al., 2007a,b, for review see: Wolf, et al., 2008). Functional complexity in the foot during walking and running was confirmed by in-vivo invasive kinematics (Arndt, et al., 2007; Nester,

et al., 2007a; Lundgren, et al., 2008) and cadaveric-model studies of foot bone motion (Nester, et al., 2007b), capturing high variability in the range of motion at inter-tarsal joints. For example, motion at the talonavicular and calcaneocuboid joints is similar to, or larger than that at the subtalar joint (Lundgren, et al., 2008). Motion between the medial cuneiform and navicular is equivalent to, or even larger than motion at the talonavicular joint (Nester, et al., 2007a,b). Recent studies also demonstrate relatively high intra-subject variability in the velocity and trajectory of the CoP (Davids, et al., 2002; Pataky, et al., 2014), and in the magnitude and distribution of peak plantar pressure in the midfoot and forefoot (Cavanagh, et al., 1998; Bates, et al., 2013b; McClymont, et al., 2016). High variability in the range of motion in the midtarsal and MTPJs, in plantar pressure in the mid- and forefoot (Nester, et al., 2007a,b; Lundgren, et al., 2008), and the statistically demonstrated causative relationship between the two (Caravaggi, et al., 2016), provide strong support for the high functional redundancy theoretically predicted for the foot (Alexander 2006).

The characteristic mean tendency of modern human midfoot mechanics is that of a rigid lateral midfoot (*i.e.*, akin to a lever) (Wolf, et al., 2008; Caravaggi, et al., 2008), compared to a characteristic mean tendency of a more compliant lateral midfoot in the other African apes (Alexander 1991). D'Août et al., (2004) reported high variability in joint segment angles at the hip, knee and ankle of *Pan paniscus* *i.e.*, bonobo, reporting

only subtle differences in kinematics and dynamic parameters during quadrupedal and bipedal walking. The authors conclude that when combined with anatomical findings, variability in plantar pressure is higher in bonobos than in humans revealing more similarities than differences in parameters during different locomotor modes, facilitating manoeuvrability and versatility in a range of behaviour. High variability in plantar pressure has also been reported in other great apes, such that there is overlap in the range of pressure between modern humans, bonobos and orang-utans (Vereecke, et al., 2003; Bates, et al., 2013b). This is supported by evidence of high lateral midfoot peak pressure in some human individuals (DeSilva and Gill 2013; Bates et al. 2013b). Midfoot sagittal-plane flexibility (Ouzounian and Sheredd, 1989; Whittaker et al. 2011), and a high range of motion during plantarflexion and dorsiflexion (>45 degrees) have been reported in humans, overlapping the range of motion observed in chimpanzees during vertical tree climbing (Venkataraman, et al., 2013a,b). Despite overlap in some parameters, it is not speculated that variation in foot structure may impact variation in foot mobility, as broader species boundaries defined by morphological and behavioural range are largely incomplete.

20.5 Functional interpretations from fossil footprints

An alternative dataset by which to interpret dynamic hominin behaviour is the analysis of fossil footprint trails. Authors have predicted

locomotor behaviour based on individual and comparative topologies, (Charteris, 1981, 1982; Bennett, et al., 2009; D'Août, et al., 2010; Crompton, et al., 2012; Hatala, et al., 2016), dynamic modelling stride lengths and leg lengths for *Au. afarensis* (AL-333-1) (Alexander, 1984; Kramer, 1999; Kramer and Eck, 2000; Sellers, et al., 2005; Crompton, et al. 2012; Dingwall, et al., 2013), and substrate effects (Behrensmeyer and Laporte, 1981; Avanzini, et al., 2008; Morse, et al., 2013; Bennett, et al., 2016; Bates, et al., 2013b). Uniquely, fossil footprint trails reflect the interaction of hominin performance with the substrate, and are the closest reflection of actual locomotor performance in the fossil record. In some cases 20 or more gait cycles are recorded as for Laetoli G-1 (Deino, 2011; Leakey and Hay, 1979; Leakey and Harris, 1987; White and Suwa, 1987), although preservation of individual prints may be variable. It is not suggested that the footprint analysis presented here can unequivocally interpret the subtle biomechanical variability present in the gait of the track maker, as only 11 footprints from the trail are analysed. Further, the dynamic interaction between the G-1 hominin and the recent ash fall cannot be directly measured from footprints, and parametric measures from dynamical systems theory cannot be applied here.

A recent contribution however, did compare 5 prints from Laetoli G-1, to prints made by modern humans, and bipedally walking chimpanzees (Hatala, et al., 2016), concluding that topological features from 5 Laetoli G-1 prints are evidence for a functionally unique locomotor

mode. Specifically the authors claim that the track maker probably walked with a more flexed knee posture, describing it as “a form of bipedalism that was well developed but not equivalent” (Hatala, et al., 2016) to that of modern humans. By contrast and through a different method, Crompton et al. (2012) had previously analysed a similar but larger ($n = 11$) dataset concluding that when substrate effects were taken into account, the Laetoli hominin prints left in the ash reflected that of biomechanically upright posture, supporting previous conclusions also drawn by Raichlen, et al., (2010). Because of this contradiction in interpretation, an extended statistical analysis of the Laetoli G-1, Ileret and Walvis Bay fossil footprint trails in comparison with experimental modern human footprints is presented here in the context of high variability in primate foot mechanics.

Here pSPM is employed as it is designed to compute measures of central tendency across multiple foot pressure images (Pataky and Goulermas, 2008). On the assumption that pressure and depth is analogous, although the analogy is limited by substrate effects, it has here been applied to footprint trails (Crompton, et al., 2012). To re-emphasize, this analogy does not imply that we believe the relationship between foot pressure and footprint depth to be linear, permitting a direct interpretation of gait from footprint depth. Nevertheless, a natural relationship must exist given that $p = \frac{F}{A}$ where pressure (p) equals the amount of force (F) (the scalar of which is measured in Pascals (Pa)) acting per unit area (A) (Giancoli, 2004). However, substrate will always

reach a point at which maximum body weight is supported, and thus, the substrate stops deforming even though pressure is still being applied. As the effect of substrate is a natural variable in studying fossil footprints, this analogue was developed to strengthen interpretations from statistical comparisons and inferences on multiple records.

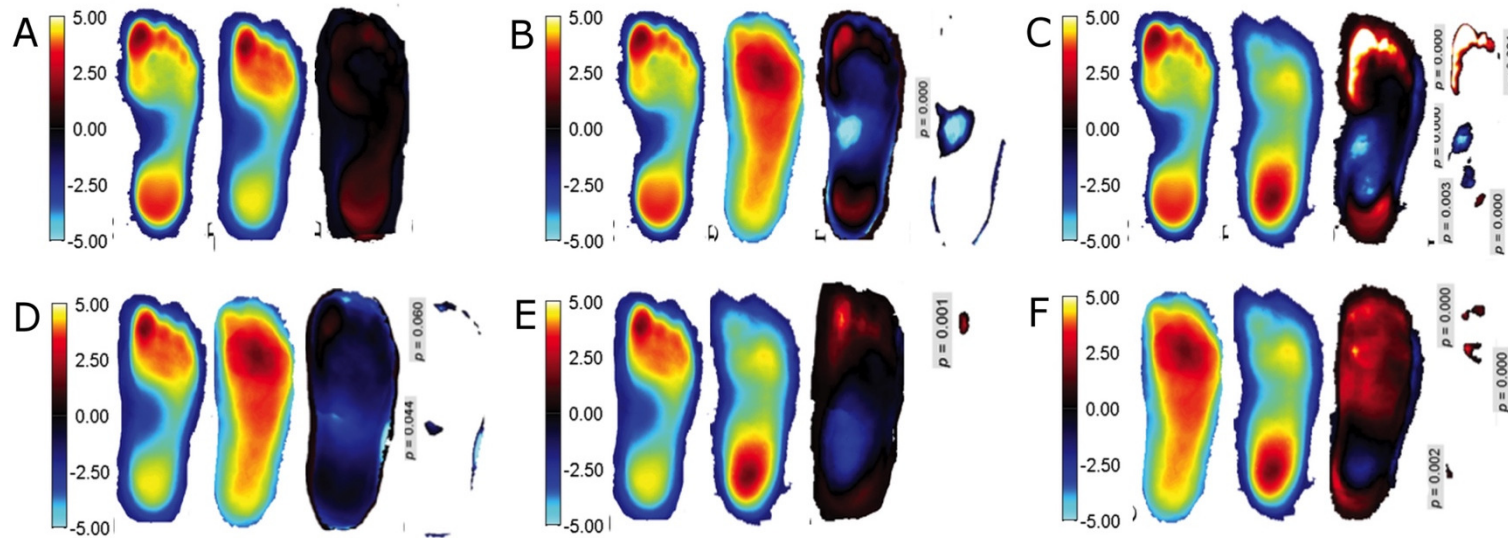


Figure 15

Statistical 'whole-foot' comparison of four footprint populations. **A.** Modern Western human mean ($n = 100$ prints from 10 individuals). **B.** Namibia mean ($n = 32$). **C.** Ileret mean ($n = 9$). **D.** Laetoli mean ($n = 11$). **E-J.** Inference plots: Columns **1** (not including **A**) and **3** (not including **C**) represent the inference maps, the subtraction of the means. Columns **2** and **4** (vertically but not including **B** and **D**) represent the probability values for areas with statistically significant differences in relative depth. **E.** Habitually shod *H. s. sapiens* versus habitually unshod *H. s. sapiens* prints. **F.** Habitually shod *H. s. sapiens* versus *H. erectus* prints. **G.** Habitually shod *H. s. sapiens* versus Laetoli prints. **H.** habitually unshod *H. s. sapiens* versus Ileret prints. **I.** habitually unshod *H. s. sapiens* versus Laetoli prints. **J.** Ileret versus Laetoli.

20.5.1 Discussion of the results

The mean images for four data sets are shown in Figure 15a-d, while statistical comparison of the samples using pixel-level pairwise t-tests (Pataky and Goulermas, 2008; Pataky, et al., 2008a) after normalization by plantar surface maximum depths are shown in E-J. These tests were carried out using the same methods used in previous studies (Crompton, et al., 2012; Bates, et al., 2013a), detailed description of all data processing, analysis, methods and methodological sensitivity checks can be found in supplementary material 16.1.1, Figures S16.1.1-6).

Habitually shod Western modern and presumably habitually unshod Holocene modern human prints show no areas of significant difference (Figure 15E). The Ileret data set differs significantly from the modern Western humans ($p = 0.000$), showing a deeper medial arch (Figure 15F). The Laetoli mean shows a significantly deeper medial arch and anterior heel impressions than the modern Western human mean, and significantly shallower hallucal impressions (Figure 15G). The Ileret footprints are significantly different from the Holocene modern humans mean, having a shallower medial arch and deeper distal toes, albeit under a small area in the midfoot ($p = 0.044$) (Figure 15H), and restricted to print edges. The latter could be the result of imperfect registration due to minor overall shape differences in the two populations, or the trackmaker

dragging the foot from the soft sediment. Most notably, the Holocene modern human and Laetoli means differ significantly in only a very small area under the distal hallucal phalanges, where the Holocene modern human is deeper (Figure 15I). Finally, statistically significant differences between the Ileret and Laetoli means exist in deeper impressions in small areas of MTH1 and distal phalanx (Figure 15J).

The statistically significant deeper medial midfoot impression in Laetoli ($p = 0.000$) than in Western modern humans (Figure 15I), also reported by Hatala, et al., (2016). likely reflects the effect of habitual shoe wearing in Western modern humans, creating a higher medial arch in this group (Stolwijk, et al., 2013). We have recently reported (Bates, et al., 2013a) that experimental studies of the relationship of footprint depth to footprint morphology show a clear tendency for deeper prints to have relatively deeper forefoot impressions. It is therefore likely that the statistically significant differences between Laetoli and Ileret (Figure 15J), and Ileret and Holocene modern human footprints (Figure 15H) sampled here, are attributable to the greater overall footprint depth at Ileret (Laetoli sample showed a mean maximum depth of 31mm, range 26-37mm; for Ileret the mean maximum plantar depth was 49mm, the range 24-94mm (see: supplementary material 19.1.2). Here, moisture content was likely higher based on sidewall suction against the foot producing long narrow tracks; by this interpretation, the moisture content likely weakened the sediment in which the tracks were made (Craig, 1997;

Bennett, et al., 2016). Similarly, the relatively greater number of deep prints from Holocene modern humans, compared to Laetoli (i.e., from wetter substrate; mean maximum plantar depth was 45mm and range 23-77 mm) could readily account for a deeper hallux impressions in Holocene human footprints.

Crompton, et al., (2012) used computer modelling to simulate contact pressures under the foot in upright and flexed knee walking. Bent knee or flexed knee walking produced higher forefoot than hindfoot pressures because of the anterior shift of the CoM. Our analysis of a larger dataset including all those analysed by Hatala and colleagues, (2016), revealed consistently deeper hindfoot than forefoot impressions, indicating full extension at the knee during upright walking (Farley and Ferris, 1998; and see Crompton, et al., 2003, 2008 on the relationship between the heel-strike transient and extended knee postures in orang-utans). There is no doubt that the Laetoli trackmaker and modern humans are biomechanically distinct: however, this does not imply different (external) function (Bock, 1965, 1994; Leland, et al., 2015). The variation in relative depth in the sequence of 11 footprints (Figure 3A) reflects similar, and thus normal biomechanical variation in stride dynamics of hominins (Figure 3B) (Alexander, 2003; Wainwright, et al. 2002), also reflecting Bernstein's description of human movement as "repetition without repetition".

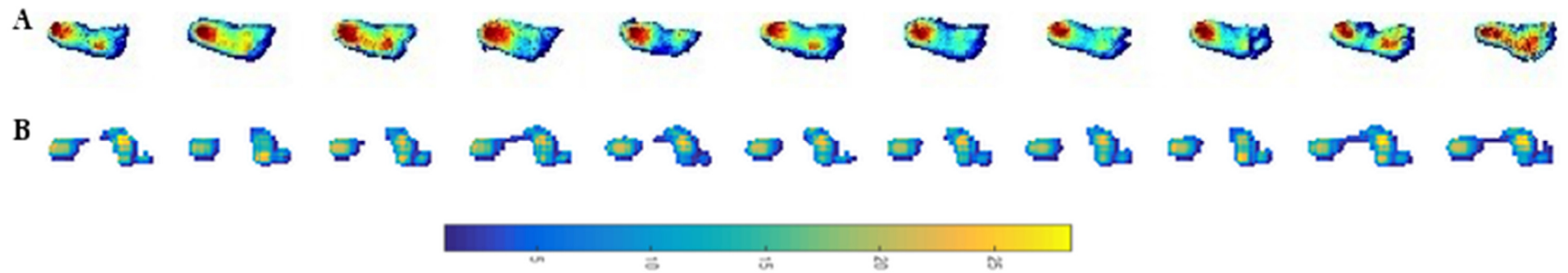


Figure 16

(A) depth maps representation of the Laetoli prints used in this analysis, showing variable distribution of maximum depth step-to-step. Greater depth is consistently focused under the heel throughout the series, but is also clearly evident under the lateral midfoot and the lateral MTH5-3 in two footprints (3, 11), and distributed under the forefoot under MTH5-2 in 4 footprints (1, 3, 10, 11). (B) 11 consecutive registered pressure images collected from a treadmill walking trial at 1.1m/s.

Figure 16 represents all prints in the Laetoli G-1 sample used in this analysis alongside 11 p-images from a pre-existing dataset of healthy subjects walking for 5 minutes on a treadmill (McClymont, et al., 2016). The human subject (B) represents the most variable subject from the human sample (McClymont, et al., 2016). While the pressure pattern in B reflects the characteristic human pattern, there is high variation in the pattern stride-to stride. This variation is not only evident in the Laetoli hominin trackway (A) but the stride-to-stride pattern is more varied, supporting D'Août and colleagues' (2004) proposal that high variability in plantar pressure in bonobos, who practice quadrupedal, tripedal and bipedal, reflects manoeuvrability and flexibility in highly varied locomotion. The human pattern, while retaining high stride-to stride variability in accordance with dynamical systems (Latash, et al., 2000; Alexander, 2003), reflects a varied, but derived locomotor pressure pattern, that would not be consistent with that of the Laetoli hominin. This figure is not a comparison of relative depths (Laetoli) and pressures (modern human), but is simply to visually demonstrate the stride-to-stride fluctuations in foot-ground interactions during locomotion, on the assumption that pressure and depth are correlated.

This assumption is made on the basis that motor control patterns adapt stride-to-stride based on interactions with the environment (Bernstein, 1967; Riley and Turvey, 2002). The expectation is that

substrate displacement would make the effect particularly marked in footprints although it is re-emphasised here that the pressure/depth relationship is non-linear. Based on the lack of statistically significant differences between Laetoli and unshod (Holocene) modern humans (Figure 15I), and the commonality of stride-to-stride and step-to-step fluctuations perceived in both trails (Figure 16a,b), there is no evidence to report that the Laetoli trackmaker utilised a flexed-knee posture beyond the range of variation that would be expected in modern humans and the time of formation of the prints examined, supporting previous results (Sellers, et al., 2005; Raichlen, et al., 2010; Crompton, et al., 2012). The EES, and dynamical systems theory, expect high variability in adaptive biological systems, permitting rapid evolutionary change (Leland, et al., 2015), and stable, functional movement (Bernstein, 1967).

Further visual inspection of the experimental footprints provided in the contribution by Hatala, et al., (2016), reveal similarities in the forefoot and hallux depths of modern human and Laetoli footprints, more so than with their selected chimpanzee footprint. The relatively deeper experimental toe depths observed in the human and chimpanzee prints, are likely due to the substrate effects described extensively by Bates, et al., (2013a), while in the human and Laetoli prints, hallucal impression indicating toe off is also clear. While not directly measuring dynamic behaviour, the unique case of fossil footprint trails is a reflection of dynamic behaviour that occurred at one time. Fossil bones however

require a different and more indirect strategy, as there is high intra- and inter-morphological variability of traits, some of which will not be functional (Bock and van Wahlert, 1965).

20.5.2 Variation in the fossil record

Darwin paid a significant amount of attention in his writings on evolutionary theory on the need to reduce the emphasis on a determinist, purely-natural selection modal perspective, in favour of a pluralistic and hence variational model that focussed on variability within species (Darwin, 1872, p. 395 discussed in Gould and Lewontin, 1979). Similarly, Griffin and Tversky (1992) suggested that palaeontological research focuses too much on the “strength of the extremeness” of morphological difference without a strong interpretive paradigm within which to interpret the observed ‘extremeness’. A recent review of taxonomic diversity in the hominin clade by Wood and Boyle (2016), presented some cases of clear evidence for species-level distinctions in morphology (e.g., between *Au. anamensis* and *Au. afarensis*), but stressed that morphological variation within hominin taxa is common, and in need of thorough assessment. They fittingly called for caution to be exercised, and for palaeontologists not to be “over-confident” in interpretations of fossil remains.

Thus, again fittingly, caution in locomotor interpretations is present in palaeontological studies: e.g., Sarrazin, et al., (2016) report

more substantial variation in thoracic shape of anthropoids (including humans) than previously expected, showing weak correlation coefficients between the upper rib cage and locomotion, and strong correlations between the lower rib cage and pelvic morphology, than to the upper rib cage. The authors conclude that in the light of this evidence, variability needs to be taken into consideration more seriously in studies of locomotor evolution. Marigo, et al., (2016) quantified inter-subject variability in the functional morphology of the calcanei and astragali of middle Eocene primates, *Anchomomys frontanyensis*, to assess its phylogenetic position compared to other crown strepsirrhines. Large statistical overlap in linear metrics of morphology within crown strepsirrhines (both living and fossil) was observed and noted; however, this overlap is not explained. Specifically, in the foot, Drapeau and Harmon (2012) plot a considerable overlap in metatarsal head torsion, between monkeys, non-human apes, australopiths and humans, and the significant overlap between species is attributed to unique differences in locomotor mode. Since metatarsal head torsion is at least in part a reflection of late-stance loading of the metatarsophalangeal joint, interpretations could be strengthened by biomechanical data that compares the percentage (and range) of stance phase where the posterior forefoot is loaded during gait. Such data would give considerably greater confidence, and indeed clarify our ability, to make such conclusions of locomotor distinctiveness.

An inadequate understanding of intra-specific and population level variation, has occasionally lead to taxonomic instability in hominoid evolution, for example the naming of a new hominin genus and species, *Kenyanthropus platyops* by Spoor and colleagues (2010, 2016) on the basis of a single, taphonomically deformed cranium. Their phylogenetic attribution was criticised by White (2003) who made strictures on the lack of attention paid to variation in palaeoanthropology. Similarly, Brunet et al. (2002) assigned the 7Ma cranium of *Sahelanthropus tchadensis* to Hominini (Brunet, et al., 2002), despite the cranium being dated within the molecular age-range for panin-hominin separation, and a distinctly panin- or gorilline-like face. The taxonomic attribution was made primarily on the basis of foramen magnum position and basiocranial/facial angles from computer reconstructions of a taphonomically deformed skull, it being assumed that evidence of orthograde was evidence of hominin affinity. Even if the latter were the case, recently Ruth et al. (2016) reported that foramen magnum angle is not correlated with locomotor behaviour in rodents, strepsirrhines, primates or marsupials.

Despite the urgings of Darwin (1872), Bock (1965) and Gould and Lewontin (1979), the study of variability within- and between-species in palaeontology, has sometimes been largely neglected in favour of comparisons of differences. The origins of such interpretations lay in the traditional pragmatic concept of the Platonic 'ideal' in the medical

sciences, from which variability represented a deviation from a defined norm. Thus, with specific reference to the foot, Elftman and Manter (1934, 1935) claimed that humans were physiologically and anatomically unable to produce a mid-tarsal break – i.e., to produce high lateral midfoot pressures such as in chimpanzees, a view which was later embodied in the Root model (1975), describing an ideal '*pes normalis*', from which substantial departure was considered an 'abnormality'. Recent work has shown that clinical flatfoot is defined by an excessively broad range of peak midfoot pressures (>200KPa Bus, et al., 2011).

However, a recent study recorded that in 5 mins of treadmill walking (this threshold was exceeded at least once in 30/45 healthy subjects (Bates, et al., 2013b). The threshold was also exceeded regularly during overground walking (DeSilva and Gill, 2013). While the Root model is no longer regarded as authoritative in podiatrics, it is still occasionally used as an interpretive framework in palaeontology. For example, Jungers, et al., (2009) claim that limited saliency in the 'cuboid peg' of the cuboid from the LB2 *Homo floresiensis* skeleton implies a bipedal gait distinct from our own; while Meldrum, et al., (2011) claim that a line in a single footprint in the Laetoli G-1 trail (G-1/26) is evidence of a midtarsal break in *Au afarensis*. Ward et al., (2011) interpreted features of a single fossil fourth metatarsal element of *Au afarensis*, as evidence for a stiff, human-like longitudinal arch facilitated by proximo-distal torsion along the metatarsal diaphysis and the orientation of the proximal and distal ends,

overlapping the human range, but not that of *Pan* or *Gorilla*. They then interpret the deep flat base and cuboid facets as functionally *unable* to produce a “midtarsal break”, which, as discussed, is common in humans (Bates et al. 2013b; DeSilva and Gill 2013). A similar interpretation is gleaned by DeSilva et al. (2010) from the cuboid facets of the StW 485 and StW 596 elements (two isolated MT4 elements from Sterkfontein), described as flat and distinctly different from the convex facet of African apes, interpreting the morphology as evidence for midfoot compliance in these specimens. Further studies of individual elements interpret convexity of the cuboid facet of *Au. africanus* (MT5 elements StW 114/115, from Sterkfontein Member 4) as being “practically identical’ to the modern human mean (DeSilva et al. 2010).

McHenry and Jones (2006) quantified variability of great toe adduction via analysis of the encroachment of the metatarsal 1 facet on the medial cuneiform in extant hominoids and two fossil hominins. Despite a hominin-fossil sample size of 2, the authors concluded that all hominins were specialised for bipedalism in possessing a highly adducted and unopposable great toe. A different conclusion might have been drawn had they had access to the then undiscovered *Au. sediba* (Zipfel et al. 2011) and the Woranso-Mille foot (Haile-Selassie et al. 2012), echoing Wood and Boyle’s (2016) warning regarding variability. The paper by Zipfel et al. (2011) on the foot and ankle of *Au. sediba* compares its calcaneal morphology (Figure 4b in Zipfel et al. 2011) to that of five great

apes, which form loosely overlapping clusters, *Au. sediba* being clustered with the *Gorillas*, again pointing to high variation in foot bone morphology. An overlap is also apparent in a more recent study of the subtalar joint of *Au. sediba* compared to eastern and western *Gorilla*, *Pan*, *Hylobates*, *Pongo*, and modern *Homo*. Here, a canonical variates analysis of nine talar and calcaneal variables shows a clear overlap in the SD between species (Prang 2016).

The majority opinion (e.g., Haile-Selassie et al., 2012, Churchill et al 2013, Zipfel et al. 2011; Green and Alemseged, 2012; Crompton, 2010, 2015; DeSilva et al. 2013; Prang et al 2016) is thus that early hominins were capable of competent terrestrial bipedalism, despite varying levels of functional traits facilitating varying ability in a range of arboreal and terrestrial behaviour. A recent paper however claims that fractures in the *Au. afarensis* skeleton AL-288-1 arose from a fatal fall from a tall tree (Kappelman et al. 2016), concluding that effective terrestrial bipedalism had already compromised arboreal climbing capacity. A more parsimonious view, supported by evidence for arboreal climbing capacity in modern *H. sapiens* in the Malaysian Batek for example (Venkataraman et al. 2013*ab*; Kraft et al. 2014), is that the hominin foot is characterized by functional redundancy sufficient to sustain either arboreal or terrestrial locomotion, with dorsiflexion angles overlapping with those of chimpanzees in vertical climbing (Venkataraman et al. 2013*ab*; Kraft et al. 2014). This ground breaking work, underlines the depth of physiological

variability evidenced in humans in a range of environments, and strongly suggests that it would be advantageous to collect similar data for non-human primates.

20.6 The variability framework

20.6.1 Collection of dynamic locomotor behaviour in living analogous species

As discussed the partial and fragmentary nature of the fossil record and the inability to collect dynamic (spatio-temporal) biomechanical data from extinct hominins immediately impede robust interpretations of function from form. The effect of the former can only be lessened with time, while a partial solution to the latter is provided by behavioural observations of, and biomechanical data collection from, living analogous primates (Foley 1992; Moore 1996). As suggested by Bock (1994), functional morphology should be closely linked to empirical ecological investigations (Moermond and Denslow 1983; 1985; Moermond and Howe 1989; Leisler et al. 1987, 1989) to clarify population level functional differences. A large part of the field of ecomorphology is the domain of “strictly nomological explanations” (Bock 1994), which can be provided in its most basic (i.e., data) form by capturing adaptive stability in primate locomotion. As mentioned briefly in the introduction and expanded upon

in section 1.1, dynamic local stability represents how quickly the system returns to normal cyclicity after a perturbation.

Analogy is of course only valid inasmuch as environments, behaviours and hence adaptations are equivalent (de Beer 1954b; Bock 1965; Gould and Lewontin 1968). Argument by analogy has a long history in palaeontology, and is most commonly achieved via: 1) observations of frequency and type of locomotor mode in the wild type (Le Gros 1924; Attenborough 1961; Petter 1962; Harrison 1963; Langham 1982; Sargis 2001; Cant et al. 2003), and in captivity (Cook 1939; Polyak 1957; Hill et al. 1957; Ulmer 1963; Stevens et al. 2008): 2) the experimental analysis of bony morphology (Carlson et al. 2005*a,b*, 2006; Carlson and Judex 2007; Carter et al. 2008; Demes et al. 2006), and 3) the collection of kinetic and kinematic parameters during a range of locomotor modes (Demes et al. 2006; Kimura 1985, 1996; Schilling and Fisher 1999; Aerts et al. 2000; D'Août et al. 2002; 2004; Vereecke et al. 2003; Blanchard and Crompton 2011; Schmitt 2011).

As noted in the introduction (section 13.1), the common chimpanzee *P. troglodytes*, was traditionally used as the analogue for hominin evolution, however later evidence revealed its derived capacity for knuckle-walking in this species (Dainton and Macho 1999, Kivell and Schmitt 2009; Isler et al. 2006; Drapeau and Ward 2007; Myatt et al. 2011, 2012). Furthermore, *P. paniscus* and *P. troglodytes* differ considerably in

limb morphology and locomotion (Zihlman and Lowenstein 1983; Kano 1992; Hunt 1994, 1996; Moore 1996; Zihlman 1996). *P. paniscus* may therefore serve as an better analogy for locomotor performance in hominins, based on closer similarities in post-cranial limb and foot bone proportions, joint segment angles and joint torques (Zihlman 1984; Zihlman and Cramer 1978, McHenry and Corruccini 1981; Kano 1992; D'Août et al. 2004; Vereecke et al. 2008). Equally, particular similarities are also obvious between humans and *Gorilla* soft and hard tissue proportions of the arm and hand, and foot (Schultz 1927; 1930).

It is reiterated here that no single species can be regarded as a perfect analogy for early hominin ancestors (Darwin 1871; Zihlman 1996; Aerts et al. 2000), but understanding the range of behaviour in relevant taxa will help to refine species overlap, to clarify individual and population level differences in function and form (Bock 1994). Notably the close morpho-functional relationships presented here between *Homo*, *Pan* and *Gorilla* represent a clade divergent from other living primates (Wood et al. 1991). Thus, establishing the range of intra-specific variability between these taxa is important for assessing variation in the fossil record (Wood et al. 1991; Wood and Boyle 2016).

Carlson et al. (2011), suggested that laboratory experiments could be refined and exported for use in the field, so that a range of behaviours can be correlated to a range of morphologies in extant primates, thus

adding to the quality of analogous datasets (Carlson et al. 2011). Data from as many relevant species as possible should be collected using standard and hence comparable methods (see e.g., Fleagle 1979; 1999; Fleagle et al. 1981; Hunt et al. 1996, Thorpe and Crompton, 2006; Blanchard and Crompton 2011). These would add to the pre-existing locomotor literature, but as discussed should ideally focus on capturing the range of variation in locomotor modes.

Palaeontologists and functional morphologists are generally lucid in their recognition of the limitations associated with collecting laboratory data (Preuschoft and Witte; Demes et al. 2006; Carlson et al. 2011). Similarly, however, natural observations in free-ranging habitats are also subject to limitations (specifically data collection) (Prost 1965; Altmann 1979; Hunt et al. 1996), but provide a unique opportunity to observe and collect a range of biomechanical behaviour unrestricted by enclosures, and, whilst in their biological role *sensu stricto* Bock and von Wahlert (1965). An excellent example of such a study is an analysis of dynamic take-off and landing kinetics in free ranging Malay colugos (*Galeopterus variegatus*) collected by the placement of accelerometers over the dorsal thoracic vertebrae (Byrnes et al. 2008). Byrnes and colleagues (2008) show that body orientation angle and peak accelerative forces during take-off to vary extensively dependent on the variability of substrate. Thus, while experimental studies of free ranging primates is fraught with difficulties, a light weight, tri-axial accelerometer (the size of a penny)

would allow field workers to establish how systems behaviours adapt step-to-step in order to maintain stability. The availability of inertial sensors that define accelerative forces unambiguously in 3D, now offers a further level of robusticity to data collection.

20.6.2 Capturing local dynamic stability

Previously (Section 19.1) local dynamic stability was discussed as a reliable, repeatable and accurate measure of stability during human locomotion (Dingwell et al. 2001), able to quantify the rate of divergence and system response to perturbations during locomotion (Rosenstein et al. 1993). As stability is not only the target of dynamic systems behaviour (Dingwell and Cusumano 2000), but is pertinent to survival in arboreal and terrestrial contexts to reduce the risk of falling. The λ is presented here as an appropriate and simple measure for stability in locomotion of analogous primate species. Based on the fundamental premise of dynamical systems to maintain stability, it is assumed to be a requirement for reproductive success in hominins.

Remote locomotor monitoring of kinetics and kinematics from inertial sensors is increasingly recommended for assessing human instability in older people (>65) (see e.g., Bolink et al. 2016), able to classify changes in behaviour from accelerometer signals (Preece et al. 2009) and wireless inertial sensors (van Shooten et al. 2011; Sloot et al. 2011; Toebe et al. 2012) for remote activity monitoring in humans.

Humans mitigate the effects of perturbations depending on the individual, for example: some will spend much energy mitigating small perturbations due to a lack of muscle strength, while others will spend less energy controlling small perturbations because they have sufficient muscle strength (Stergiou and Decker 2011). Finally, individuals can control small perturbations effectively, but stability is perturbed by higher magnitudes due to reduced range of motion at joints (Bruijn et al. 2013).

Humans are generally more sedentary than non-human primates, but there is abundant anecdotal evidence that suggests other great apes suffer from obesity and chronic musculoskeletal effects in captivity when a naturalistic locomotor activity is not simulated by the environment (Grether and Yerkes 1940; Maple 1982; Quick 1984; Pruetz and McGrew 2001; Young 2003; Hill 2004; Hosey 2004; Honess and Marin 2005; Garner 2006; Carrasco et al. 2009; Fabregas et al. 2011). The extent to which chronic illness and disease effect stability during locomotion in non-human primates is not as established to the same extent it is in humans. Thus, while there are varying aspects that influence stability, it is reasonable to begin with λ and variations in the fluctuations of SI, and the response to varying environmental supports, and the type of perturbations encountered as these will differ from those experienced by humans.

Primate ecologists have adapted this approach to include body-mounted sensors for remote monitoring of locomotor activity in lemurs

(Sellers and Crompton, 2004) and colugos (Byrne et al. 2008), however not to measure stability. The precise advantage of measuring stability by λ is that it can be calculated from any kinematic data, regardless of reference frame (Dingwell and Cusomano 2000). The λ plots the relative position of state space represented in multiple consecutive time series, i.e., the trajectory of the CoM in Euclidian space during locomotion, capturing the instantaneous response of the motor system to perturbations, to maintain stability during locomotion. A Global False Nearest Neighbours (GFNN) analysis compares the distance of deviations between neighbouring trajectories (Rosenstein et al. 1993; Dingwell et al. 2001; Bruijn et al. 2013). This allows the researcher to specify a minimal temporal separation of nearest neighbours in a particular dimension. A positive λ indicates divergence of two initially neighbouring trajectories, rendering the system unstable (Rosenstein et al. 1993; Dingwell et al. 2001; Bruijn et al. 2013) (see: supplementary material 19.1.3.1).

Compared to the placement of motion capture video cameras, sensor placement is less sensitive and thus less problematic in wild settings. As noted also by Bruijn et al. (2013), trunk kinematics were found better able to differentiate stability in older and younger people, than lower limb kinematics (Kang and Dingwell 2009). With the rapid miniaturization of remote sensor devices, it is suggested that small skin mounted – (with future potential for subcutaneously injectable) inertial sensors to be placed over the, 1) dorsal thoracic and 2) sacral vertebrae, to

provide a robust measure of stability of the CoM and the trunk segment. As discussed, accurate measures of stability are achieved by assessment over at least 20 gait cycles (Dingwell et al. 2001; Bruijn et al. 2012; Njagarah et al. 2013), as increasing data series length is accompanied by an increased precision in λ (Bruijn et al. 2009). In practical terms, 20 consecutive cycles might appear daunting in a field situation; however, many primates do tend to use regular routes through home ranges (Thorpe and Crompton 2006). Therefore, placement of wireless receivers within range of such standard routes is feasible and renders a requirement for collection of 20 cycles achievable. The suggested method also enables the simultaneous collection of SI parameters that define speed i.e., $v = \frac{d}{t}$ where d is derived from the SL defined as the distance travelled between two consecutive heel strikes of the same foot, and t , is the SF, the rate of time it takes to complete a stride (Alexander 2003). This satisfies Alexander's (2003) definition of a stride as 'a complete cycle of movement, for example, the time between one foot-ground interaction and the next of the same foot, or "the distance travelled in one stride' (p. 87 and see also p. 107, 2003).

D'Août et al. (2004) collected these parameters, including joint and segment angles, and vGRF data in *P. paniscus* during a variety of locomotor modes. High variability in locomotor mode and performance parameters was reported, supporting previous authors suggestions that locomotion in *Pan* is 'unconstrained' when compared to humans (Crompton et al. 1998;

Vereecke et al. 2003; D'Août et al. 2004). It is accepted that flexibility in locomotor performance encourages variety in locomotor modes, including a range of arboreal styles (D'Août et al. 2004). In modern Western humans, variability in SI parameters, and joint and segment torques, are restrained as would be expected in a highly specialised and derived gait (Pailhous and Bonnard 1992; Hausdorff et al. 1995, 1996; Dingwell and Cavanagh 2001; Dingwell et al. 2001; Frenkel-Toledo 2005; Dingwell et al. 2006; Jordan et al. 2006; England and Granata 2007; Jordan et al. 2007a,b).

Fluctuations in SI are governed by fractal-like properties, whereby long-range (Power Law) correlations and memory reveal a self-similar pattern in fluctuations that are statistically related to ones preceding it over multiple other time scales (West and Griffin 1999; Hausdorff 1995, 1996, 2005). As discussed in humans, this pattern is interrupted when walking to a metronome, suggesting supraspinous neural networks determine the long-range fractal fluctuations of gait timing in humans (Hausdorff et al. 1995; Gates and Dingwell 2009; Richardson et al. 2004). The same effect is also evident in mice with neurodegenerative disorders (Amende et al. 2005), as has been established as an underlying rhythmic alteration of movement patterns in all vertebrate locomotion (Grillner 1985). When movement control patterns are impaired by disease or captivity, fluctuations in SI alter along with multi-scale locomotor dynamics (Goldberger et al. 2002; Hausdorff et al. 1995, 1996). While it is not directly possible to “distract”

primates with a metronome during locomotion, each primate will demonstrate intra- and inter-subject variability in SI relative to the individual, the choice of mode and the substrate, based on the laws of dynamical systems, but also likely by long-range correlations.

Thus, high variability is expected if not based only on the wider range of locomotor modes available to analogous primates, but also, stable CoM and trunk segment trajectories (Rosenstein et al. 1993; Dingwell et al. 2001; Bruijn et al. 2013), represented by negative (stable) λ and high variability in the fluctuations of SI (D'Août et al. 2004). This prediction is subject to change with time as locomotor boundaries may be more clearly defined and understood as frequency and preferred locomotor habits become more apparent.

20.6.3 Observational locomotion

Current studies of primate locomotion in the field characteristically gather information from support characteristics (diameter/orientation), in relation to each locomotor bout (Hunt et al. 2006; Fleagle and Mittermaier 1980; Gebo and Chapman 1995; Thorpe and Crompton 2006; for review see: Blanchard and Crompton 2011). Definitions of locomotor modes are usually defined by biomechanical characteristics (Hunt et al. 1996; D'Août et al. 2004), relative to support orientation (in 3D). The percentage use of supports during each locomotor mode, and the type of supports used during each locomotor bout may be calculated using pre-

defined locomotor categories (Boinski 1989; Britt 1996; Cannon and Leighton 1994; Crompton 1980; 1984; Hunt et al. 1996). The contribution of each locomotor mode contributes to each kilometre of travel, providing estimates of daily energy expenditure (Fleagle 1976; 1977; Warren and Crompton 1998).

There are limitations however that accompany observational studies, namely the accuracy of determination of step-parameters e.g., step length and width, leap length and trajectory. By conducting observational research alongside 3D video photogrammetry and inertial sensors, based data collection of stability during movement, we would expect to establish stronger estimates of the forces and costs involved in non-human primate locomotion and thus a better understanding of how primates evolved to move around different environments. For example, Sellers and Hirasaki's (2014) 3D photogrammetry software is designed to capture 3D branch/support motion as well as limb motion, and thus the response of the primate neuromuscular system to factors such as changing surface friction or type, branch diameter and rebound i.e., perturbation, could be accurately assessed through relative displacement of the branch and the subject in 3D.

This should be accompanied, as is current standard practice in locomotor ecology, by observations of activities such as feeding, foraging and escape behaviour that impact the traditional biological role of

locomotion. Additionally, it is essential to establish the natural occurrence of supports themselves (n support type per linear, square or cubic metre) within the field site to be able to assess a species' or individuals support preferences (Britt 1996; Blanchard et al. 2015). This is of particular importance as Britt (1996) established that transects and area counts are not sufficient parameters to establish choice of locomotor mode.

Current observational studies typically already compare locomotor behaviour between sites in the same species, or between individuals in the same site. These are sufficiently comprehensive in the assessment of variation in locomotor mode and support use based on examples from a range of primates (e.g., Cant et al. 1992; McGraw et al. 1996; Cunha 2006; Craul et al. 2007; Blanchard et al. 2011), but could be enhanced with 3D video photogrammetry (Sellers and Hirasaki 2014: open source software available at: www.animalsimulation.org). This system is self-calibrating based on the distance separating the cameras, able to generate absolute magnitudes, and capture a range of performances in 3D overcoming sub-optimal data collection from 2D technology.

With placement along habitual daily routes, cameras can be positioned to accurately capture a wide field of view to record variable behaviour and track the position of the accelerometer. Quantification of trunk kinematics and stability by λ in 3D space will provide the opportunity to quantitatively test model predictions and provide real

world spatial inputs for modelling primate enclosure use (Ross et al. 2011). Further, it will provide insight into lifetime performance constraints such as the effect of neuromuscular decline on stability in primates with age (Berg et al. 1997; Herman et al. 2005; Pijnappels et al. 2008). Collection of stability data using surface mounted or eventually subcutaneous sensors, as proposed, would be difficult and probably unethical in completely wild populations. However, the number of sites worldwide at which zoo-bred, (or confiscated captive primates kept as pets), are being rehabilitated prior to final release is growing exponentially. The reintroduction candidates are often electronically monitored, and the collection of stability data as proposed above could thus be both practical and ethical, as it would provide invaluable information to conservationists on the success of rehabilitation and the choice of reintroduction sites to maximize naturalistic behaviour.

20.6.4 Functional morphology

Bock (1965) described adaptations as features that contribute to performance capacity during its lifetime in a given environment. Physiological and morphological features may be neutral in effect: i.e., we cannot assume that morphological differences universally imply performance or behavioural uniqueness (Bock 1965; Gould and Lewontin 1978). Despite the challenges associated with interpreting function from form, Wainwright et al. (2014) and others (Karr and James 1975; Bock 1994; Norton et al. 1995; Plummer et al. 2008) have correlated variation

in locomotor performance against morphological variation and environmental niche, in aquatic, avian and reptilian species. There have recently been studies of intra-and inter-specific geographic and ecological variation in *Gorilla* limb and foot bones by Tocheri and colleagues (2011) and Jabbour and Pearman (2016), however the substantial altitudinal effects on expressed locomotor behaviour of *Gorilla* was not fully considered (Crompton 2015). Further, neither attempted to analyse the extent to which morphological variation of specific features was associated with performance distinctions, as is standard practice in ecomorphology (Wainwright et al. 2014). This follows the suggestion of Bock (1994) that ecomorphology would be an appropriate strategy employed by functional morphologists. An excellent example by Wainwright and colleagues (2002) showed how the variability in pectoral fin aspect ratio affects swimming performance of labrid fishes, and consequently trophic effectiveness in highly variable reef microhabitats.

Establishing the range of variation in morphological parameters in living primates seeks to understand how small differences in morphology may affect performance, and performance, in turn, reproductive success in a given environment. The appropriate calculation for intra- and inter-variability in morphology is the CV ($CV = \frac{SD}{m}$), that would focus analyses of large data sets toward establishing the range of morphology, but also in establishing large datasets that are statistically comparable to human datasets. This calculation has been considered in

several studies in palaeontology, outlining intra-specific variation in dental morphology of higher primates (Wood et al. 1991), cranio-dental parameters to predict the location on the skeleton where high intra-species variation may occur (Wood and Lieberman 2001), and long bone cross-sectional geometry and body size in five species of indriid (Demes et al. 1991).

Several components of an interpretive framework built on the variability omnipresent in biological systems have been presented here as a combined framework to enhance our understanding of hominin locomotor evolution. The variability framework is comprised of three parts: 1) biomechanical data is represented by local dynamic stability (λ) collected from 2 tri-axial accelerometers placed over the distal and proximal vertebral column, and from SI parameters (SL and SF) from 3D video photogrammetry (Sellers and Hirasaki 2014). 2) Collection of these data may be best performed in rehabilitation centres, near forest environments where ecological interactions and therefore biological role may be observed (Bock 1965). Further, this would advance our understanding of the effects of ageing on stability during locomotion, providing further insights into the effects of ageing in modern humans. 3) Variation in morphological parameters (CV) of living analogues, would establish the range of form in living primate analogues, strengthening interpretations of morphological distinctions in the fossil record (Wood et al. 1991; Wood and Boyle 2016; Alexander 1984; 1994). A long-term goal

of this framework would be to establish similar sample sizes and depth of understanding of primate biomechanics and motor control in living analogous species, to those already available to humans. This knowledge would greatly enhance our understanding of the evolution of locomotion form and function from a fragmentary fossil record.

20.7 Locomotor plasticity

Developmental or phylogenetic plasticity is the capacity for change in a phenotype relative to the environment (Laland et al. 1999, 2001; 2015). While plasticity hypotheses are long established in evolutionary biology (Via and Lande 1985; Schlichting 1986; Sterns 1989; Pigliucci 2009; Odling-Smee et al. 2003; Laland and Sterelny 2006; Pigliucci and Müller 2010; Danchin et al. 2011; Dickens and Raham 2012; Blanchet et al. 2014; Laland et al. 2015), there is little reference to it in hominin palaeontology due to contention in the role plasticity plays through phenotypic and genetic accommodation (Pfennig and McGee 2010; Moczek et al. 2011) i.e., the adaptation of parts in response to environmental constraints independent of genetics. However, plasticity has been shown to advance diversity in niche construction in unique environments (Odling-Smee et al. 2003), encourage population level connectivity and gene flow (Crispo 2008), and increase the probability of shifts in adaptive peaks, radiations and speciation events (Price et al. 2003; Lande 2009), contributing to the spatio-temporal variation in

selection parameters (Huey et al. 2003; Duckworth 2009; Cornwallis and Uller 2010).

As the fossil record expands with time, interpretations have exposed functional overlap extending from the Lower Pliocene (*circa* 4.4 Ma) to the Late Miocene (*circa* 7 Ma) reflecting plasticity. During this time period, hominids displayed a combination of plesiomorph and apomorph characteristics (Lovejoy et al. 2009ab; Senut et al 2001). Equally during this period, there was an affinity for high biodiversity in ecological zones that was typical of protohominins as well as early hominin environments, such as those ascribed to *Sahelanthropus tchadensis* (Brunet et al. 2002ab, 2008). Complex environments such as these would also be expected to exert selective pressure for locomotor plasticity to exploit, varied, unstable and rapidly changing microhabitats. Myatt and colleagues (2010, 2012) have demonstrated that the ranges of muscle cross sectional area and fibre lengths of great apes in general, overlap considerably with each other, implying that their length/tension and torque/joint angle capacities also overlap. This may be surprising given the ecological and locomotor differences in all species of primates identified in field-studies.

Regarding fossil species, Haile-Selassie et al. (2012) found the ratios of the fourth metatarsal of the Woranso Mille *Australopithecus* foot to fall with *Gorilla*, recalling claims of similarities of limb morphometrics in *Gorilla* and modern humans (Schultz 1927, 1930). Further, scapulae of

Gorilla and *Pongo* are very similar in morphology to *Au. sediba* (Churchill et al, 2013) and to the Dikika *Au. afarensis* specimen (Alemseged et al. 2006), further suggesting that hominins and non-human great apes overlapped in their locomotor performance capacity.

Traditionally greater adduction of the hallux in ‘mountain’ *Gorillas* reported by Schultz (1930) was attributed to terrestriality, and the view that mountain *Gorillas* were largely terrestrial based on reports from Karisoke. However, the extent of what we know about *Gorilla* locomotor behaviour has recently been increasingly challenged more recently (for review see: Crompton 2015). Remis (1995, 1999) observed that habitat structure and resource availability exerts substantial influence on *Gorilla* locomotion. The author (Remis 1999) suggests that locomotion exhibited at sites like Karisoke, is adapted to a locally extreme high-altitude dwarf forest environment, however Karisoke and nearby sites in the Virungas lie between 2700 and 3400m. However, the ‘mountain’ *Gorillas* population in the Bwindi Impenetrable Forest, live in forest at altitudes of 1160–2607m, much closer to altitudes for lowland *Gorillas*, e.g., those at Bai Hokou forage at 463 m, where arboreal fruit is more abundant and readily exploited (27% of observation days according to Robbins and McNeilage, 2003).

The framework presented here, combines methodological aspects of ecomorphology, but focussed on defining stability as a measure of

reproductive success as it is in humans, to help clarify such issues of locomotor capacity versus expressed niche exploitation in living analogous primates. As much as possible this data should be collected while in the context of its biological role (Bock and van Wahlert, 1965), and thus while exploiting a range of locomotor frequency and type over a diverse range of supports while foraging, finding mates, and avoiding predators: and this range should be compared between diverse sites. In the case of 'mountain' *Gorillas* an ecomorphological perspective suggests that variable hallux orientation allows closely related populations to exploit widely differing habitats, with differing opportunities for climbing. A parallel exists in humans: DeSilva (2009) presented data from chimpanzee and human distal tibial morphology, to argue that human morphology could not sustain sufficient dorsiflexion to allow chimpanzee like vertical climbing. A later and largely ecomorphology-focussed study however, found that indigenous arboreal foragers do produce chimpanzee like kinematics in vertical climbing (Venkataraman et al. 2013*a,b*). Subsequently, DeSilva collaborated with Venkataraman to combine their individual approaches with field ultrasound techniques, establishing that changes in fibre length of gastrocnemius in habitual arboreal forages, adequately offset any derived features of the ankle associated with bipedalism (Venkataraman et al. 2013*b*). It is suggested here that the range of both the orientation of the hallux in *Gorilla*, and of gastrocnemius fibre length in humans, are evidence for the existence of locomotor plasticity in living hominoids.

We have seen that it is recently more widely accepted that fossil foot elements representing a ‘mosaic’ picture of foot evolution from 7MA to present, probably facilitated hominin locomotor abilities in terrestrial and arboreal environments (Zipfel et al 2011, Haile-Selassie et al 2012; DeSilva et al. 2013). As described by geneticists discussing the hereditary nature of movements (Johnson and Edwards 2002), a variety of genes interact in a variety of ways to influence biomechanical function, but they do not fully determine it. It is important to consider that the underlying dynamics of locomotion must be broadly similar in hominoids defined, and where possible quantified by nomological adaptations (Bock 1965). This supports the view that the equal interaction of nature and nurture provides performance constraints on locomotor behaviour, making plasticity the selective target for hominin locomotion.

20.8 Conclusions

In this chapter, examples have been presented to show that the hominin foot is characterised by high functional redundancy, interpreted as serving the adaptive goal of locomotor plasticity. We have provided evidence that variable motor patterns are based on underlying similarities present in all moving dynamic systems, and reflected in the diversity of form and function. Some contradictions, and occasionally deterministic interpretations are present in fossil (Jungers et al. 2008; Ward et al. 2011;

Spoor et al. 2010; 2016), and fossil footprint trail interpretations (Meldrum et al. 2009; Hatala et al. 2016). Specifically, footprint trails represent the dynamic interaction with the ground, and suggest that in cases where substrate effects are strong (Bates et al. 2013a), that the variability in the topology plantar surfaces *is* the characteristic feature of hominin gait and should be quantified as far as is possible by dynamic locomotion in living analogues.

The majority of modern locomotor interpretations from fossil hominins attribute the intra-subject morphological variability and intra-species behavioural variability, to either locomotor plasticity (Crompton et al. 2010; Blanchard and Crompton 2011; Myatt et al. 2010; 2011) or argue that observed mosaicism of traits permits a range of arboreal and terrestrial activities (Zipfel et al. 2011; DeSilva et al. 2013;). The two are essentially equivalent, except that here it is contextualised by adaptation, whereby locomotor plasticity is the target of natural selection, facilitating locomotor specialisation in primates in the cyclically changing micro-habitats in Africa in the Plio-Pleistocene in line with previous hypotheses in evolutionary biology.

20.9 Materials

20.9.1 Materials and methods

Illet prints used in this analysis are from the upper footprint surface at FwJj14E (4° 18' 44" N; 36° 16' 16" E) and include five prints from the longest trail (FUT1-1, FUT1-3, FUT1-5, FUT1-6, FUT1-7), two prints from a shorter trail, (FUT3-1, FUT3-2) and four individual prints (FUI1, FUI2, FUI6, FUI7). They were imprinted in fine-grained tuffaceous silt and fine sand deposited as overbank flood deposits and assigned to *Homo erectus* based on biometric inferences of body mass and stature (Bennett et al. 2009). The Laetoli prints (Leakey and Harris 1987) (Trail G-1) used here are scans of first-generation casts of the Laetoli G-1 prints at the National Museum of Kenya, laser-scanned using a Konica-Minolta VI900 with a vertical resolution of 90µm. Prints G-1/28 and G-1/30 were omitted due to excessive erosion and vegetation damaged, and also G-1/38 as the posterior-heel imprint is missing through faulting (Crompton et al. 2012). On the edge of the Namib Sand Sea (Walvis Bay, Namibia) unshod footprints from the Holocene (11,500 Ka) (Kineham 1996; Morse et al. 2013) occur on silt surfaces, deposited as overbank flood deposits from the Kuiseb River and exposed between sand dunes (23° 00' 25" S; 14° 29' 26" E). These prints were excavated in 2010 and scanned using a Konica-Minolta VI900 (Morse et al. 2013). The print makers are assumed to have been habitually unshod due to their African context and date, as well as the presence of skin (callus) texture visible in the footprints

(Kineham 1996; Morse et al. 2013). If footwear was worn on occasions it is unlikely to have been laterally constrictive. Optical laser scans of 100 prints from ten living, Western individuals, made in a laboratory tray filled with fine, moist sand, were recorded using an LDI PS-400, and the ten-subject means combined into an overall modern human mean (Crompton et al. 2012). Photographs and stereopairs of individual Laetoli prints are available in the Laetoli monograph (Leakey and Harris 1987), scans of both the Laetoli and Ileret prints have been previously published (Bennett et al. 2009; Crompton et al. 2012) and the prints from Namibia have also been well documented (Kineham 1996; Morse et al. 2013). Consequently, the replication of individual print images here would be redundant.

All footprint scans were rectified to the orthogonal plane and cropped so that only the plantar surface of each footprint was retained (Figure S19.1.1). After removal of any additional surrounding sediment, the data was imported as XYZ point clouds into Matlab and processed using Liverpool's in-house software pedobarographic Statistical Parametric Mapping (pSPM) (Pataky and Goulermas 2008; Pataky et al. 2008a). This software was designed to compute measures of central tendency across multiple foot pressure images (Friston 1995; Pataky and Goulermas 2008), however by substituting pressure for depth it has here been applied to footprint trails (Crompton et al. 2012). This substitution does not imply that the relationship between foot pressure and footprint depth is linear, permitting a direct and simple (yet

potentially biomechanically incorrect) interpretation of gait from footprint depth. Nevertheless, a natural relationship exists given $p = \frac{F}{A}$ where pressure (p) is the amount of force (F) acting per unit area (A). With each step, the point at which the substrate is strong enough to support body weight and resists deformation despite the continual application of pressure, is highly variable due to the variable nature of substrate.

The pSPM software co-registers the entire plantar surface of a sample of footprints such that each pixel (footprint depth) corresponds to the equal anatomical location in all co-registered images. To achieve standardized comparisons, all point clouds were down-sampled into images of 1mm² pixel dimensions. To enable standardized comparison of footprints of different absolute depths, each image was normalized by its own maximum depth such that pixel values ranged 0-1, with zero corresponding to shallowest depth, and 1 the point of maximum depth of the footprint as in our previous study (Bates et al. 2013a). Registration of images within pSPM can be undertaken using a number of automated algorithms or through manual manipulation that involves the rotation and scaling of individual images to a common template image (Pataky et al. 2008b). A previous study tested the accuracy and repeatability of manual registration and showed that it produces comparable, and in some cases better results than various registration algorithms (Pataky et al. 2008b). Where a higher level of divergence in topology occurs, such as with inter-

species comparisons, manual registration has been found to give better results (Crompton et al. 2012).

In this analysis topological variation required that the 9 Ileret prints were manually registered to each other, as were the 11 prints used from the G1 trail (Crompton et al. 2012). The Walvis Bay and modern human footprints were internally registered using an automated algorithm that minimized the root mean square error of pixels globally across pressure images (Pataky and Goulermas 2008). Registrations between populations of prints, facilitating cross-site (i.e. cross-species) comparisons and were all performed manually. Here, all manual registrations were repeated three times to observe any impact of operator subjectivity on subsequent statistical tests (Figures S19.1.1- S19.1.6).

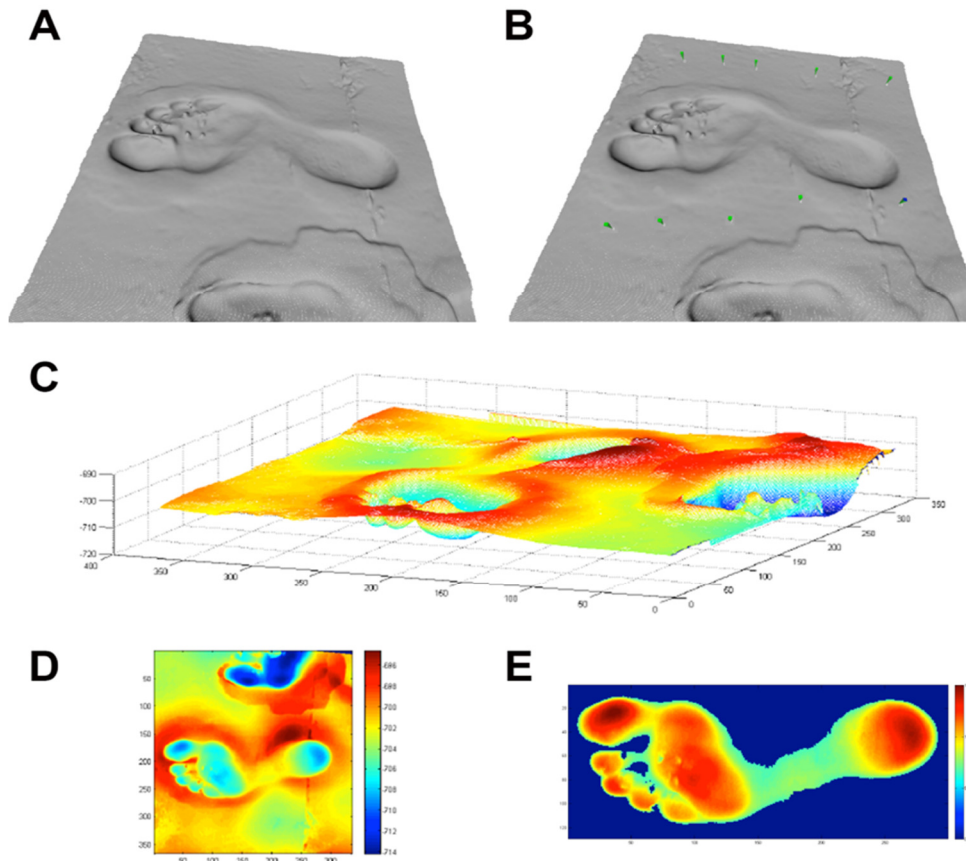


Figure S20. 1

Diagrammatic explanation of the data processing carried out prior to registration and topological statistical analysis. A, Surfaced laser scan of modern human footprint. B, 10 points were selected on the under-formed surface surrounding the print (i.e. outside any displacement rims, fractured areas etc.). A plane was subsequently fitted through these points and (C) the rotation required to align this plane with the horizontal was applied to the footprint, thereby aligning print depth with the vertical axis. D-E, The same horizontal plane was then lowered until it reached the highest topological point (i.e. shallowest depth) on the plantar surface of the footprint. All pixels above this plane were then cropped out leaving only the plantar surface (occasionally small surrounding areas of sediment were manually removed). Depth normalization was then carried out using the range of depths present across the plantar surface, culminated with a scaled depth range of 0-1, with the shallowest point (within the mid-foot in E) having a value of 0 and the deepest point (in the

hallux in E) having a value of 1. In plate D, the areas in red surrounding the print, become areas of blue the surround the print in plate E.

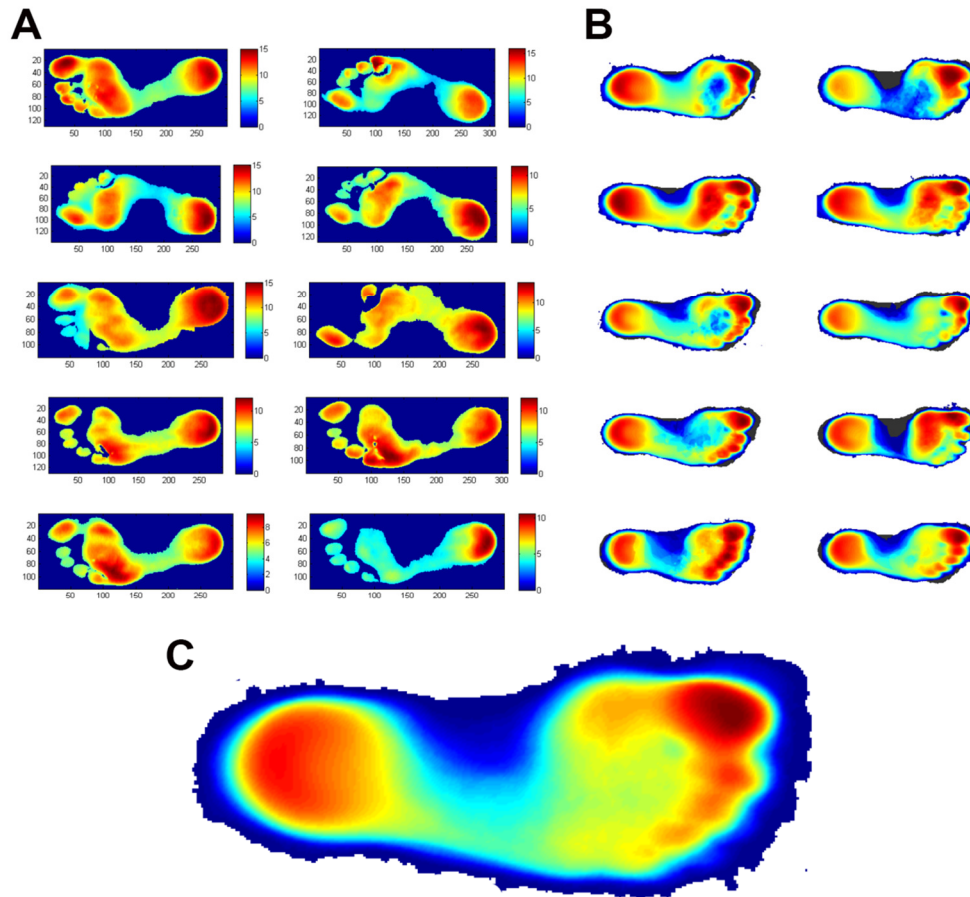


Figure S20. 2

An example of within-subject registration using 10 prints from the modern, western human data set. A) The 10 prints are pre-processed as explained in Figure S19.1. An initial registration is then performed that individually (i.e. one-at-a-time) aligns the last 9 prints with the first print in the data set (not depicted above). B) Subsequently a second registration is performed in which all 10 prints are individually (i.e. one-at-a-time) aligned with their mean image. C, is the mean image itself. For the modern western human and Namibian prints this was carried out using automated algorithms.

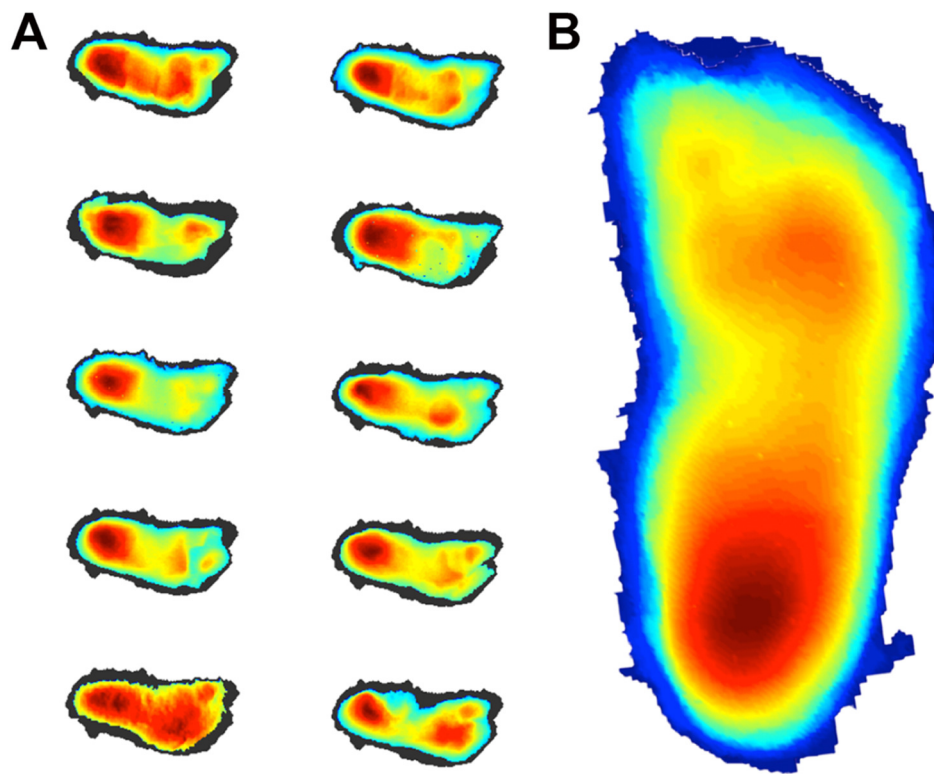


Figure S20. 3

Depiction of the same registration process shown in Figure S19.2 for the Laetoli prints, in which registration was carried out manually (operator rotation and scaling of images) rather than using automated algorithms. The same manual registration was necessary on the Ileret prints.

Neighbouring pixels tend to behave in a similar way due to the nature of interconnected systems such that the t -values from each pixel form a generally smooth SPM, which can be shown to be topologically characteristic of a registered SPM dataset (e.g., cluster size, number of clusters, etc.). Aspects of random field theory are used to determine the t -

threshold at which $\alpha = 5\%$ of the pixels would be expected to reach by chance, based on the smooth bounded shape of the footprint, and parameterized by pixel connectivity across the plantar surface. Shape information is necessary because a square field, for example, would be expected to produce fewer supra-threshold clusters than would a long, narrow rectangular field of the same area and same smoothness. The SPM is then thresholded based on this critical t -value, and one is left with some supra-threshold clusters of pixels that have survived the threshold. Random field theory then uses analytical probability density functions to compute the likelihood that clusters of the given size could have been produced by chance (Friston 1995; Pataky and Goulermas 2008).

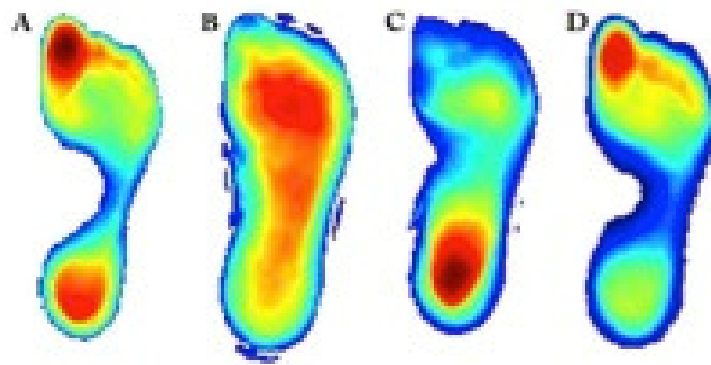


Figure S20.4

Nonlinear registration modern human (A), Ileret (B) Laetoli (C) and Holocene human (D) means that are then registered to the Namibian mean. The individual prints are re-registered to the non-linear mean templates and the means regenerated.

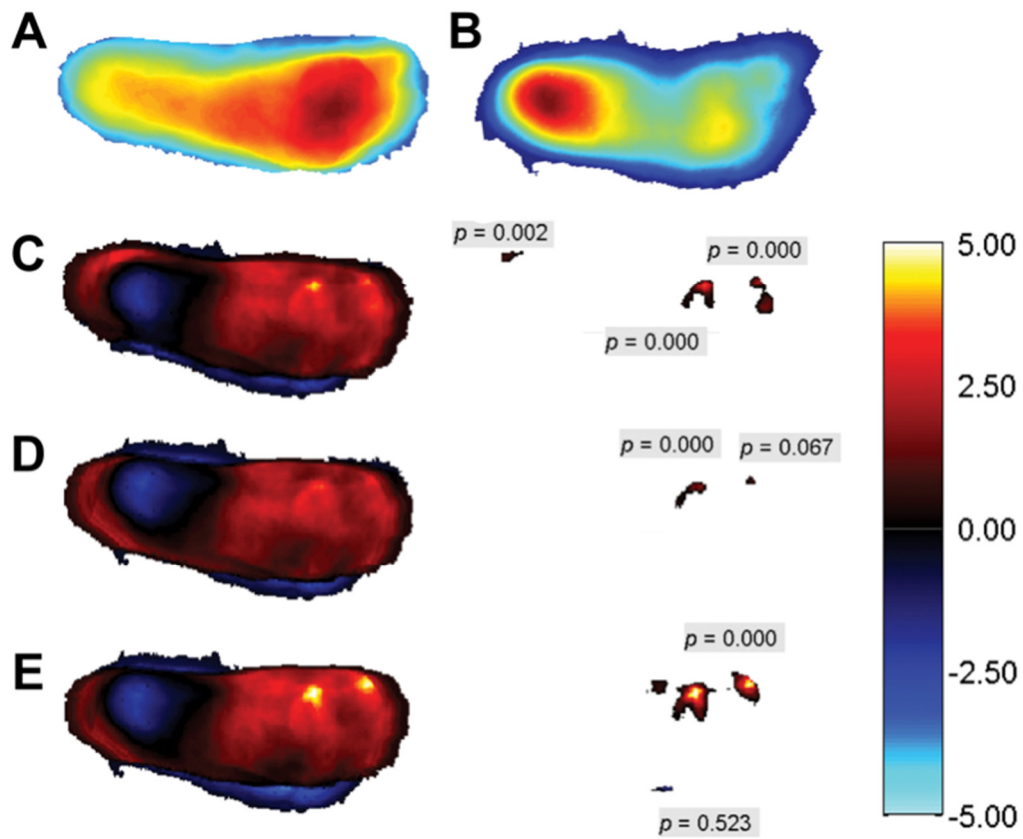


Figure S20.5

The intra-operator repeatability test on all inter-site manual registrations via manual linear registration revealed that only the Ileret and Laetoli data sets were susceptible to minor variation in levels of statistical significance under slightly different manually defined registrations.

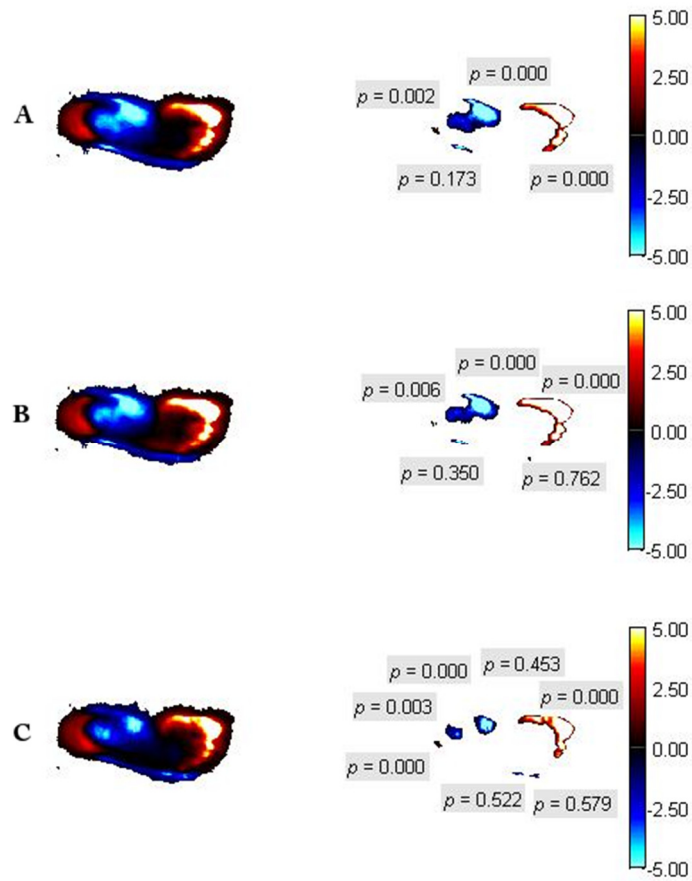


Figure S20.6

Subtraction of means plot, for 3 alternative sets of means of 5 registered prints from the 11-print dataset of the G-1 trail to modern humans. A) the earliest 5, B) the middle 5, and C) the last 5, to the modern mean after registration. In this analysis, modern humans consistently have a deeper impression in the forefoot than that of the Laetoli hominin, irrespective of the footprint selected. C) Laetoli is consistently deeper in the midfoot and anterior heel, but the size of significant supraclusters are significantly reduced. The choice of prints therefore slightly influences the size of the area that is relatively deeper.

20.9.2 Additional footprint discussion

Comparison of footprint topology between sites with different substrates and geological properties is potentially difficult since the biomechanical signature of a print maker is mediated through the geotechnical properties of the substrate, and the substrate may also influence taphonomic modification (Craig 1997; Ditchfield and Harrison 2011; Liutkus-Pierce 2013). In this analysis, print populations from three natural environments at the micro-scale (pixel level), two from silt-rich flood/overbank deposits (Namibia and Ileret: (Crompton et al. 2012; Bennett et al. 2009) and one from volcanic ash deposited via air-fall at Laetoli (Leakey and Harris 1987), with a sample of modern prints collected from fine sand in the laboratory. At the micro-scale, variation also exists within each depositional environment, dependent on local variations in grain-size, moisture content, vertical stratigraphy and significantly (especially the case at Laetoli), the degree of turbation by animal trampling (Morse et al. 2013). Substrate affects are particularly obvious in the Ileret prints, whereby withdrawal of the heel from soft, wet substrates causes side-wall suction, naturally decreasing the macro-shape, specifically the width of the print (Craig 1997; Bennett et al. 2009; Morse et al. 2013).

Maximum plantar print depths for our Laetoli sample showed a mean of 31 mm, range 26-37 mm; for Ileret the mean maximum plantar depth was 49 mm, the range 24-94 mm; and for Walvis Bay (Namibia) the

mean maximum plantar depth was 45 mm and range 23-77 mm. The mean depth of the experimental modern Western prints was 34 mm, with a range 24-42 mm. Technically, the substrate first holds the weight of the individual during the first phase of stance, only to fail further during the second phase associated with higher plantar pressures during toe-off. The lack of clarity of toe impressions is a feature of deeper prints where foot withdrawal often modifies the impressions left by phalanges (Crompton et al. 2012). This is particularly evident at Ileret where toe-drag is clear, associated with higher forces required to pull the toes out of deeper substrate. The medial longitudinal arch is also modified in softer substrates by the proximal movement of sediment under rotation of the ball of the foot, potentially producing a tendency towards a flatter arch in deeper prints.

However, the methodology used in this analysis helps mitigate these influences. Principally, we are able to compare whole footprint populations on the basis of measures of central tendency rather than by comparing individual prints, which may show strong individual substrate influences (Leahey and Harris 1987; Bennett et al. 2013; Morse et al. 2013). For cross-site comparisons it subsequently becomes important that the range of sedimentological properties exhibit overlap (i.e. in terms of their geomechanical strength), thereby isolating biological (anatomy and gait) similarities and differences that impact on footprint form. It is important to note that these sedimentological conditions may not directly

or obviously translates into sediment characteristics that are easily measurable in the geological record, such as average grain size, sorting or composition. Broadly similar geomechanical properties (e.g., bearing capacity, Poisson ratio etc.) may be produced by different combinations of physical sediment characteristics (Craig 1997). There is no doubt that further experimental work is needed to explore the influence of sedimentology on footprint form (and the range of variables that define a sediment's rheology). However, in the absence of this experimental work, and a detailed mechanistic understanding, it is perhaps most appropriate to ensure comparisons are made on prints of overlapping depths since depth does appear to correlate with substrate strength (Bates et al. 2013a; Morse et al. 2013).

21. General discussion

21.1 Background

This chapter will evaluate the four pieces of research presented in chapters 17-20. This background section is first focussed by a short contextualisation of the background to the thesis topic (section 21.1), followed by a wider discussion and critique of each chapter's conclusions (21.2-21.4). Finally, general limitations and future direction of the project are presented and discussed (21.5).

An area of mathematics called dynamical systems theory describes the behaviour of complex dynamical systems by differential and difference equations (Beltrami 1998). The theory captures and equates the long-term quantitative behaviour of dynamical systems, quantifying the momentary adaptive solutions that solve equations of motion occurring as a function of time (Lerner and Trigg 1991). Understanding foot ground interactions is of course underpinned by all of Newton's laws of motion, however the second ($F = m * a$) is the most relevant. For example; a p-image is comprised of n vector values (p), that capture the amount of force (F) acting per unit area: (A) ($p = \frac{F}{A}$). The unit area is defined both by the size of the pixel (0.717cm^2) and bounded by footprint size and shape, which is itself highly varied in humans. Pressure values, and composite p-images, are thus dependent on the force, mass and speed applied by the

foot to the pressure plate. Newton's third law (Resnick et al. 1992) would also be appropriate ($P_1 = -G_2$), and has been assessed using pSPM analysis (Pataky et al. 2010, 2014).

Chapter 17 characterised the magnitude and spatial distribution of peak pressure variability by the MSE and CV. Chapter 18 explored the strength of increasing and decreasing linear trends in peak pressure with a wide range of treadmill walking speeds, and from by a large individual trial n . Chapter 19 employed a random subsampling analysis to quantify the average by which the MSE varies as individual sample n increases or decreases at a range of walking speeds. Chapter 20 argues that locomotor plasticity is a selective target in hominin evolution ensuring reproductive success, based on the high variability in biological systems, and suggest a variability framework to test this argument when considering hominin locomotor evolution.

21.2 Combined discussion and limitations, chapter 17 and 18

Chapters 17 and 18 assessed different aspects of peak and mean pressure variability with a range of walking speeds. The magnitude and spatial distribution of variability by the MSE characterises highest variability in pressure under the MTH5 and MTH1 in all subjects, with occasional occurrences in the heel and no relationship to speed (Figure 7, 9). This prompted a combined comparative analysis of discrete topological speed comparisons of the whole foot, and traditional linear regression of

mean and peak pressure metrics, which was also applied topologically by pSPM to the whole plantar surface (Figure 7). Briefly, while the CV was also calculated by pSPM, the regions with high variability were clustered with areas of low pressure (and vice versa), a finding also reported by Cavanagh et al. (1998). Therefore, in these experiments CV is not determined as an accurate calculate or spatial variability for peak pressure when visualised as variation maps (Figure 8).

It is clear that pressure increases under MTH1 and decreases under MTH5 with walking speed in 10 out of 16 subjects, where highest variability is also identified (Figure 7, 9). However, the subject with the highest overall MSE (subject G), only display statistically significant differences between discrete walking speed comparisons in only two cases, at the most disparate walking speed comparisons i.e., 1.1m/s vs. 1.7m/s, and 1.1m/s vs. 1.9m/s and then, only in the heel (Figure 10, see: supplementary material, Figures S17.3-S17.4). Furthermore, the subject with the highest mean and maximum metrics (Table 5, subject E) only reported statistically significant differences at 4 out of 10 discrete walking speed comparisons (see: supplementary material, Figures S17.1-S17.10). That variability is highly localised, but low, and that the range in maximum and mean pressure is high, but shows no correlation to walking speed, implies highly complex and coordinated neuromuscular behaviour facilitating adaptive, and unique patterns of interaction in the foot complex. This relationship requires further investigation perhaps with

reduced sensation by local anaesthetic on healthy subjects to assess the response of pressure variability to reduced sensation.

This finding is consistent with Cavanagh et al. (1998) who were unable to discriminate between the pressure patterns of diagnostic groups, when calculating variability by the MSE or CV. The authors report that areas of highest variation are associated with joint regions that exhibit frequent ulceration (MTH1 and hallux). The aetiology of ulceration however, is highly complex as patients with high pressure under MTH1 and hallux do not always develop ulcers, and conversely patients with moderate peak pressure under MTH1 and hallux can ulcerate (Veves et al. 1992). Barn et al (2015) reported poor and moderate correlations between 5 predictors of foot pathology and deformity and peak pressure, supporting previous studies of patients with diabetes, that report only moderate correlations between peak pressure and plantar foot lesions (Armstrong et al. 1998; Lavery et al. 2003; Vevus et al. 1992; Yavuz et al. 2008, 2017). The effectiveness of predicting plantar lesions depends on thorough understanding of plantar soft tissue mechanics and the biomechanical etiology of foot ulcers (Yavuz et al. 2008). It has been reported that during gait shear forces are induced in the plantar tissue at twice the frequency of peak pressure (Yavuz et al. 2008). Shear stress acts tangentially in the anteroposterior and mediolateral directions, constructing complex stress-strain patterned behaviour in the sublayers of the plantar tissues (Yavuz et al. 2017), inducing greater breakdown

than the applied vertical load (Delbridge et al. 1985). The location of ulcers and calluses have been linked to the distribution of excessive shearing in the plantar tissues (Lord 2000; Davis 1993; Akhaghi and Pepper 1996; Brand 2003; Sanders et al, 1998) resulting from high frictional forces (Yavuz et al. 2007). Excessive friction and shear forces have been shown to cause hyperkeratosis in both humans and other animals (Goldblum and Piper 1954; MacKenzie 1974) and are widely accepted as indicators of plantar ulceration (Yavuz et al. 2017). The measurement of shear pressure in the plantar tissues requires the measurement of normal local and tangential forces simultaneously. Future work should consider the spatio-temporal variability in pressure and shear stresses and fatigue characteristics in young children and in habitual vertical climbers, and habitually barefoot populations.

The results presented here report numerous spatial combinations of increasing and decreasing pressure with walking speed for each step. If high internal and external motion, force and pressure relationships are to be assumed here, as they have been reported in the literature (Lungrand et al. 2007; Nester et al. 2007a,b; Barn et al. 2015; Caravaggi et al. 2016), then the increasing pressure occurring posterior to the toes (section 17.?, Figure 7, 9, see: supplementary material S17.1 – S17.10), can be interpreted as a reflection of the high variation in inter-tarsal joint range of motion in humans (Lundgrund et al. 2008; Nester et al. 2001, 2002, 2007a,b). Such functional interconnectedness would support highly

redundant and complex physiological units during highly adaptive patterned state-spaces during mid-stance, facilitating smooth locomotor behaviour on a treadmill (Turvey 1990; Latash et al. 2000). These interpretations further support high mechanical redundancy reported for the human foot (Bernstein 1967; Alexander 2003). That statistically significant differences in speed in the mid-and forefoot are reported only at the most contrasting speeds, represents the efficiency by which healthy and unperturbed motor systems achieve stable treadmill walking at a range of walking speeds. This is supported by universally low CV (<2%) in peak plantar pressure, confined almost exclusively to the area of the plantar surface with the widest surface area, MTH5 and 1, and the complete lack of relationship to speed (Figure 12).

21.3 Discussion and limitations from chapter 19

To quantify the average by which the MSE varies as individual sample n increases or decreases in plantar pressure analyses by pSPM (chapter 19).

Chapter 19 explored the range at which the MSE varies in response to changes in n via a random subsampling analysis. Treadmill effects are discussed in more detail than in preceding chapters in section 21.5.3. Results report that the range in MSE is high when individual trial n is low ($n = <100$), concluding that in healthy subjects, the presence of high

variability in peak pressure, requires large individual trial n to capture the habitual pressure pattern. pSPM is widely used in the biomechanics literature (Pataky et al. 2008, 2010, 2011, 2013, 2014; D'Août et al. 2009; Keijsers et al. 2009) as are Monte-Carlo simulations (Mello et al. 2003; Torrence and Butler 2006; Ribiero et al. 2009). This method is most similar to that employed by Pataky et al. (2010b) in that pSPM and 1000 Monte-Carlo simulations were employed in both studies. 1000 Monte-Carlo simulations via SPM in a finite element model of heel skin indentation, indicated increased signal sensitivity to broadly spanning stress responses at the heel compared to previous simulations (Erdemir et al. 2006), but no significant field-wide effects, supporting previous work (Erdemir et al. 2006). However, this chapter 19 represents the first study to combine these analyses for application to peak pressure.

The findings suggest that in this experiment, between 350 - 450 (see: supplementary material, Figures S18.5–S18.8) steps are necessary to reliably capture (within 5%) of the range of variability present in >500 steps, at the range of walking speeds analysed here. Useful comparisons can be made to a study that explores the sensitivity of measures of variability in kinematic parameters, that suggests >400 steps reliably estimate the running functions (running mean and running SD) from step length, width and time (Owings and Grabiner, 2003; Hausdorff et al., 2007). The experimental method employed in chapter 19, and that used by Owings and Grabiner (2003) differ in outcome parameters. They

estimate the number of steps required to establish mean and standard deviation in cases where either a narrower (2SD) or a wider (3SD) SD is tolerable. Results showed that more steps were required (>400) for narrower distribution tolerances of the MSE. This same premise is established for measures of stability (e.g., λ , mFM) (Rosenstein et al. 1993; Dingwell et al. 2001). While variability and stability measures are similar, they quantify different aspects of gait, thus stability is not discussed explicitly here, but is well represented in the literature (Springer et al. 2004; Dingwell et al. 2001; Hollman et al. 2010; Young and Dingwell 2012; Konig et al. 2014; Bruijn et al. 2009; Riva et al. 2014).

This study is relevant only qualitatively to the clinical literature in providing a useful baseline by which to appreciate how many steps it requires to capture the range of habitual variability in peak pressure parameters by MSE. The suggested 400 steps is not practical for clinical trials of pathological or aged individuals. Highly variable results can be attributed to a range of challenges associate with clinical trials, access to space and technology, experimental conditions, and patient constraints: i.e., physical capacity, ability and pain avoidance. Thus, experimental protocols (e.g., pressure plate, two-step protocol), methodology (e.g., pressure plate, in-shoe data), outcome measures (e.g., habitual peak pressure, effect of ulceration on peak pressure), subject health (e.g., pathological, non-pathological), individual trial n and analytical approaches (e.g., regional masking, pSPM) (Arts and Bus, 2011; Kernozek

et al., 1996; McPoil and Cornwall 1999; Cavanagh et al. 1998; Springer et al. 2004; Dingwell et al. 2001; Hollman et al. 2010; Young and Dingwell 2012; Konig et al. 2014; Bruijn et al. 2009; Riva et al. 2014). However, a compromise between accuracy and trial constraints is important to consider.

Results from this large walking speed trial n and those of Cavanagh et al. (1998), suggest that 3-12 steps would not reliably characterise habitual behaviour in peak pressure. Particularly in clinical practice, the ability to track system adaptation over time is essential to understanding how the system responds to intervention and treatment. The results in chapter 19 could potentially be extrapolated to clinical trials, with the option of collecting sets of small individual trial n from 1 minute of comfortable treadmill walking over multiple days. Unless in situations where fractal dynamics are being assessed, the effect of treadmill walking on reducing variability in kinematic parameters could be sacrificed in healthy populations, to gain larger samples of individual speed trial n . This would facilitate a greater understanding of how systems with restricted motor control (e.g., patients with diabetic neuropathy) interact with the environment and change over time, allowing greater insight into the neurological control of gait behaviour in humans.

21.4 Discussion and limitations of chapter 20

This chapter presents a qualitative application of the dynamical framework underpinning high functional redundancy in anatomy, and, the pattern of movement in humans as evidenced by high intra-subject, and inter-subject variability in biomechanical parameters, to explain the high inter-species variability apparent in fossil hominin record. Chapter 20 used pSPM to conduct comparative analysis between fossil and modern human footprint trails by substituting relative pressure for depth to allow cross-population comparisons. The aim was to verify claims that biomechanical differences could be detected within the topology of fossil footprints that suggest the Laetoli G-1 trackmaker practiced a mechanically distinct gait from modern humans (Hatala et al. 2016).

The results in chapter 20 do not support any meaningful statistically significant differences in the pattern of footprint depth or topology 3.66MA, that are not accountable to substrate effects. While using a different method, Bennett et al. (2016) arrived at essentially the same results, but implied functional stasis in foot function in hominins. Chapter 20 argues rather, that the lack of statistically significant results is largely a product of substrate effects and small individual trial n , acting to increase the appearance of the variability (Pataky et al. 2013). Furthermore, considering the high variability in plantar pressure in primates (Vereecke et al. 2003; D'Août et al. 2004; Bates et al. 2013b; McClymont et al. 2016), healthy humans (Figure 9; see: supplementary

material, Figures S17.12 – S17.20) and, in humans where sensorimotor feedback signals are greatly reduced but with no associated reduction in variability (Cavanagh et al. 1998), potentially deny accurate functional interpretation from footprints, at least as proposed by Hatala et al. (2016).

It was not the goal of this chapter to devalue the locomotor assumptions that accompany interpretations of morphology, but to suggest that the variability framework would provide a more robust assumption, supported by ecomorphology and dynamical systems theory. It was also not the goal of this chapter provide a tutorial on the calculation or analysis of the λ , and the reader is directed to Brujin et al. (2013). Part of the variability framework includes the use of photogrammetric 3D reconstruction technology to track locomotor mode and support use, while inertial sensors (tri-axial accelerometer, magnetometer and gyroscope), simultaneously track the motion of the trunk segment. The accuracy of an analysis of stability via λ , requires each trajectory to begin within the same state space. In all field work situations, there are numerous limitations that must be overcome in order to ensure accuracy. Specifically here, to collect the valid number of consecutive strides (20) necessary to calculate λ . 3D video photogrammetry reconstructs environment fields of view based on light and background texture within the field of view, assuming an initial set of camera parameters, calculating the error between image coordinates into 3D space (Sellers and Hirasaki 2014). Poor light and low contrast reduce the strength of the

reconstruction, but high texture contrast between images, as would be more readily available in rehabilitation centres, facilitating calibration due to multiple consistencies in shared fields. Considerable care will be required to ensure optimal conditions at the start of the simultaneous recording from inertial sensors and multi-camera video to ensure maximum clarity of image and thus assure that trajectories begin in the same state space.

21.5 Limitations and future directions

21.5.1 Calculators of variability and stability

A complete description of stable gait pattern behaviour requires an understanding of how single strides are generated, how movements throughout the stride are controlled and how they adapt across multiple strides (van Emmerick et al. 2016). This is achieved by calculators of variability and stability.

Linear methods interpret biomechanical data through linear correlations thus the central premise of dynamic movement is that intrinsic system dynamics are influenced by small changes that have small effects (Kantz and Schreiber 2004). Some early studies propose that various aspects of variability indicate stability (Winter 1989; Yack and Berger 1993), and later, increases in locomotor variability representing a

reduction in the complexity of the system have been reported to correlate with falls risk in the elderly (Maki et al. 1997), and with degenerative basal ganglia disorders (Hausdorff et al. 1998).

Variability in gait is commonly analysed by normalising and averaging data from both within a stride, i.e., a pixel, or all pixels in a p-image; and variability between strides, e.g., step length or stride time, usually reporting linear effects (Dingwell et al. 2001; van Emmerick et al. 2016). While variability is often equated with stability, variability is not a measure of the euryphysiological response that maintains stability (Dingwell et al. 2001; Bruijn et al. 2013; van Emmerick et al. 2016). Thus, there no interpretation regarding the role of the feet in balancing the body over the base of support during breaking and propulsive procedures, are beyond the scope of this thesis.

21.5.2 Variability in plantar pressure

Despite differences in kinematic behaviour in populations, and unique modifications to gait made by individuals, pressure distribution reflects the ultimate mechanical interactions driving individual steps at the foot ground interface, showing minimal change except when mechanical and physiological walking is stressed by high velocity (Figure 10). However, results from chapter 17, combined with those of Cavanagh et al. (1998), suggest that variability in plantar pressure is largely unaffected by unique mechanical constraints (e.g., speed and neuropathy),

as no correlation was reported here (Figure 7). Thus, the sensitivity and validity of variability in peak plantar pressure as a measure that can interpret neuromuscular behaviour, remains to be determined.

This is not to suggest that aspects of variability are not useful indicators of population boundaries or movement patterns (chapter 20), but that variability in plantar pressure is so necessarily high, that unique mechanical differences are not expressed significantly in pressure by the techniques employed herein. This extends to footprint analyses where mechanical differences could not be detected between topological surfaces spanning 3.66MY (chapter 20; Figure 15, 16). As discussed, high variability in pressure could represent the highly efficient, patterned behaviour of human walking, that is itself derived and less variable than other primates (D'Août et al. 2004). It is assumed here that pressure patterns in primates would be more variable (as it is in kinematic parameters [D'Août et al. 2004]), in both magnitude and spatial distribution, than the derived obligate bipedal pattern observed here, at the distal, lateral and medial boundaries posterior to the phalanges and hallux. A similar assessment on population specific healthy cohorts e.g., habitually arboreal modern humans (Venkataraman et al. 2014), non-pathological flatfooted populations (Stolwijk et al. 2010) would be valuable in increasing the predictive strength of plantar pressure for future use, and relationships between internal function and external pressure patterns.

Standard deviations measure the average differences between stride parameters, or step nodes, and are commonly perceived as independent from the cumulative effects of temporal order in which strides occur (Dingwell et al. 2001). To measure stability, information must be gleaned from the systems momentary response to perturbations. This is considered a more precise measure of stability (Dingwell et al. 2001) able to be contextualised by dynamical systems theory, to understand how systems (i) maintain their current state, (ii), transition between states and (iii), utilise fractal dynamics to quantify interactions across varying spatio-temporal scales and levels of invariance of multiple process (van Emmerik et al. 2016). Variability in plantar pressure could be better interpreted when combined with measures of stability during continuous walking on a treadmill and overground. This would include the collection of kinematic and kinetic parameters including trunk fluctuations in the CoM by λ , stride length, time and width. A multidisciplinary approach may improve the interpretive power of plantar pressure as a measure of stability.

Such an analysis would require a wider catchment of speeds, specifically speeds below that of 1.1m/s presented here. Time-series data are dependent on the relative timing of different gait phases, and are strongly correlated with walking speed. Also, the relative time-series of p-images would be useful in assessing changes in pressure variability over

time. Data collection at a slower velocity e.g., 0.5m/s, would provide better insight into mechanisms in the foot that adapt and transition to maintain stability within- and between-strides at speeds that would be potentially unstable to a healthy young human. Specifically, it has been shown that at speeds below 0.5m/s the relative timing of gait phases is liable to considerable influence variability (van Hedel et al. 2006). Future projects would extract the λ for the analysis of variability in (i) peak pressure, step width, step time, impulse, CoP, and vGRF by pSPM, (ii) joint kinematics, particularly flexion/extension at the knee and ankle to determine dorsiflexion angle, (iii) tri-axial accelerometer to measure 3D movements of the CoM about the base of support at slow (0.4m/s, 0.8m/s,) and fast speeds (0.9m/s), (iv) EMG firing patterns of lower limb musculature, specifically, *m. rectus femoris*, *m. vastus medialis*, *m. vastus lateralis*, *lateral and medial hamstrings*, *m. tibialis anterior*, *m. gastrocnemius medialis*, and *m. adductor hallucis*.

Variations in stride length and stride time and gait speed, demonstrate an underlying fractal-like property (Hausdorff 1995; Hausdorff 1996; West and Griffin 1999; Griffin et al. 2000; Terrier et al. 2005). Specifically, these parameters function by long-range correlations, what might be described loosely as “memory”, such that perturbations that occur during walking are statistically related to previous effects occurring over multiple time scales (Hausdorff 2005). Over time, disease and ageing can disrupt motor control pattern behaviour, increasing

fluctuations that accumulate in effect during gait (Hausdorff 2005; Jordan et al. 2007). For example, in older people, variability in stride length and time by the λ (Dingwell et al. 2001) and a decrease in step width by CV (Owings and Grabiner 2004), correlate strongly with an increase in the risk of falls. Variability also increased in frontal hip and knee motions, internal and external knee rotations, and trunk motion (Kang and Dingwell 2008) further decreasing stability and increasing the risk of falls. Inclusion and analysis of stride length, stride time and stride width parameters by λ would increase the interpretive power of chapters 17 and 18, and similar sensitivity analyses as in chapter 17 conducted to establish the relationship to plantar pressure – which has not yet been attempted. Other parameters such as variability in the trajectory of CoP and vGRF, under different substrate and shoe compliance conditions, would also be a future direction of such a study. CoP trajectories reflect the dynamic interaction between the foot and the ground (Cavanagh and LaFortune 1980; Chrisholm et al. 2011; Pataky et al. 2014), however the variability of the relationship between CoP and vGRF, their trajectories and the effects of overground walking are yet to be determined. Inclusion of these parameters in future studies would assist in determining the mechanisms controlling stability at the foot ground interface during gait.

Finally, the data collected for this thesis did not tightly control for dual tasking effects or, head and eye movements. The universally low and spatially consistent trends in variability with walking speed presented

here do not suggest that the data was adversely affected by this feature of the data collection, and is justified here. Studies have demonstrated that attention to cognitive tasks during walking reduces control over speed in both young and older adults (Ebersbach et al. 1995; Abernethy et al. 2002; Gage et al. 2003; Beauchet et al. 2005), although the effect is less in younger adults (Yogev-Seligmann et al. 2010). During data collection, subjects were allowed time to become comfortable with the treadmill at each speed before data collection began, and were instructed to look at one spot on the wall approximately 5 metres ahead of the treadmill. Variability in peak pressure reported here is universally low ($CV = <2.5\%$) (Figures 5, 6) reflecting efficiency in locomotor performance in young, healthy adults and shows no reliably consistent linear relationship with speed. However, an increase in the variability of peak pressure calculated by MSE with an increase in the level of difficulty associated with varying cognitive tasks has been made evident (Webster et al. *in prep. a-c*). Future analyses should control for the effects of dual tasking to further delineate the neuromuscular characteristics interpreted from plantar pressure.

21.5.3 Treadmill effects

Control of speed varies radically by populations, and the effect of speed on variability in kinematic parameters is well established. The results of chapter 18 reveal that speed should be controlled relative to the unique constraints of the study. Studies of the effect of walking speed on

gait parameters generally control for $\pm 5\%$, however here they were controlled for $\pm 20\%$ (increments of 0.2m/s). Statistically significant differences in peak plantar pressure between speeds was most common at speeds that were most different to each other. This reflects the highly entrenched control patterns during normal walking, while collection of slower speeds (0.4m/s), may have provided more interesting yet indirect assessment of the control of gait by measure of variability.

Treadmill walking has been shown to reduce kinematic variability (Pearce et al. 1983; Arsenault et al. 1986; Wank 1988; White 1998; Dingwell et al. 2001). The reliability of measures of variability are also further reduced when made from individual sample $n < 120$ strides (Hollman et al. 2010; Riva et al. 2014), as local stability is shown to collate over multiple consecutive strides (Dingwell et al. 2001). Thus, studies often employ the use of a pressure sensitive or normal treadmill to collect large individual trial n . Debate is ongoing as to the effect that treadmill walking on the natural variability present in overground walking, with some studies reporting no differences (Pearce et al. 1983; Arsenault et al. 1986; Wank 1988; Dingwell and Cavanagh 2010). A more recent modelling study confirms that humans exploit redundancy during treadmill walking to simplify motor control patterns by strongly regulating goal-relevant fluctuations (Cusumano and Cesari 2006), ignoring non-task specific variability (Dingwell et al. 2010). Specifically, stride length and stride time were adjusted based on a hierarchy of short-

term (maintenance of walking speed) and long-term (reducing energy costs) achievement goals (Dingwell et al. 2010). This mechanism allows the neuromuscular system to maintain balance and stability during treadmill walking, and should be discussed in future analyses that involve treadmill walking. Future studies should also include a large dataset (>400 p-images) of consecutive steps in overground walking to account for differences that occur during foot-ground interactions in different conditions for example; the effect of different shoe materials and sole characteristics over substrates of variable compliance, in different populations both habitually shod and unshod, healthy, and those with pathology or older adults.

22. General conclusions

1. No linear relationship between variability in peak pressure by MSE with speed was detected by whole pressure field analysis.
2. Highest variability in pressure was confined almost exclusively under MTH5 and MTH1.
3. The overall variability in peak plantar pressure however is universally low ($CV = <2.5\%$), reflecting the efficiency of the locomotor system during controlled treadmill walking, but potentially reduced further by the effects of treadmill walking. High redundancy, and coordinative patterning capacity selects different combinations of motor patterns to produce the least variable set of kinematic and kinetic behaviour for each step.
4. Pedobarographic statistical inference regularly reports clusters of increasing peak pressure with speed under the heel, MTH1 and phalanges in most subjects (10/16). Observed differences in the distribution of pressure between subjects reflects the unique combinations of motor control pressure patterns and biomechanical etiology.
5. Pedobarographic statistics report clusters of decreasing pressure with speed to varying degrees under the tarsal-metatarsal complex, longitudinally along MT5-3, and localised under MTH5-2. Differences between subjects reflect the unique combinations of motor control pressure patterns.
6. Differences between pixel clusters in the mid- and fore-foot consistently only reached levels of statistical significance in speed comparisons of the highest disparity.

7. The relationship between peak pressure magnitude with walking speed is characteristic of medial column force transfer in humans, progressing from the hind-foot to the hallux, however this general trend is fundamentally characterised by highly variable relative contributions of soft and hard tissues both within and between individuals in this sample.
8. The range in MSE is exponentially sensitive to individual trial n . The large individual total trial, and individual speed trial n in this thesis ensures interpretations made throughout chapters 17-20 by the MSE are statistically valid.
9. Topological statistical inferences of footprint analyses spanning 3.66MY report no statistically significant differences in footprint surface depth as an analogue for peak pressure, that could not be attributed to substrate effects.
10. The range (SD) in peak pressure is high, both within and between subjects reflecting the range in internal constraints available to, and acting upon the foot-ground interface in each subject i.e., high adaptability is assumed from high variability, within the theoretical context of dynamical systems theory.
11. The efficiency by which animals locomote is a testament to the complexity of biological systems, and the neural networks that continuously update movement patterns relative to external conditions. High intra-subject variability in pressure reflects high redundancy and adaptability of the whole foot, and is a characteristic of non-human primate feet.
12. Based on the results in chapters 17-20, it is hypothesised that high variability in peak pressure, and in locomotor patterns in general, is a strong selective pressure for locomotor plasticity by natural selection in

the hominin clade. This hypothesis should be tested by a multi-disciplinary approach that combines complimentary aspects of dynamical systems theory, ecomorphology, evolutionary biology and functional morphology, as is developed and presented in chapter 20 under the variability framework.

23. Supplementary materials

23.1 Chapter 18 supplementary material

The following chapter represents the figures produced from each pressure vs. speed comparison made at all speeds across all subjects. The topological pressure records (S18.1-S18.10) represent the mean p-images from each speed comparison and the probability map distinguishing pixel level significant differences in the variability of pressure with speed. The bar graphs (S18.11-18.15) represent the discrete analysis by pSPM plotting changes in mean and peak pressure at different walking speed trials. The two tests were carried out to demonstrate the differences between linear and topological analyses of peak plantar pressure with speed.

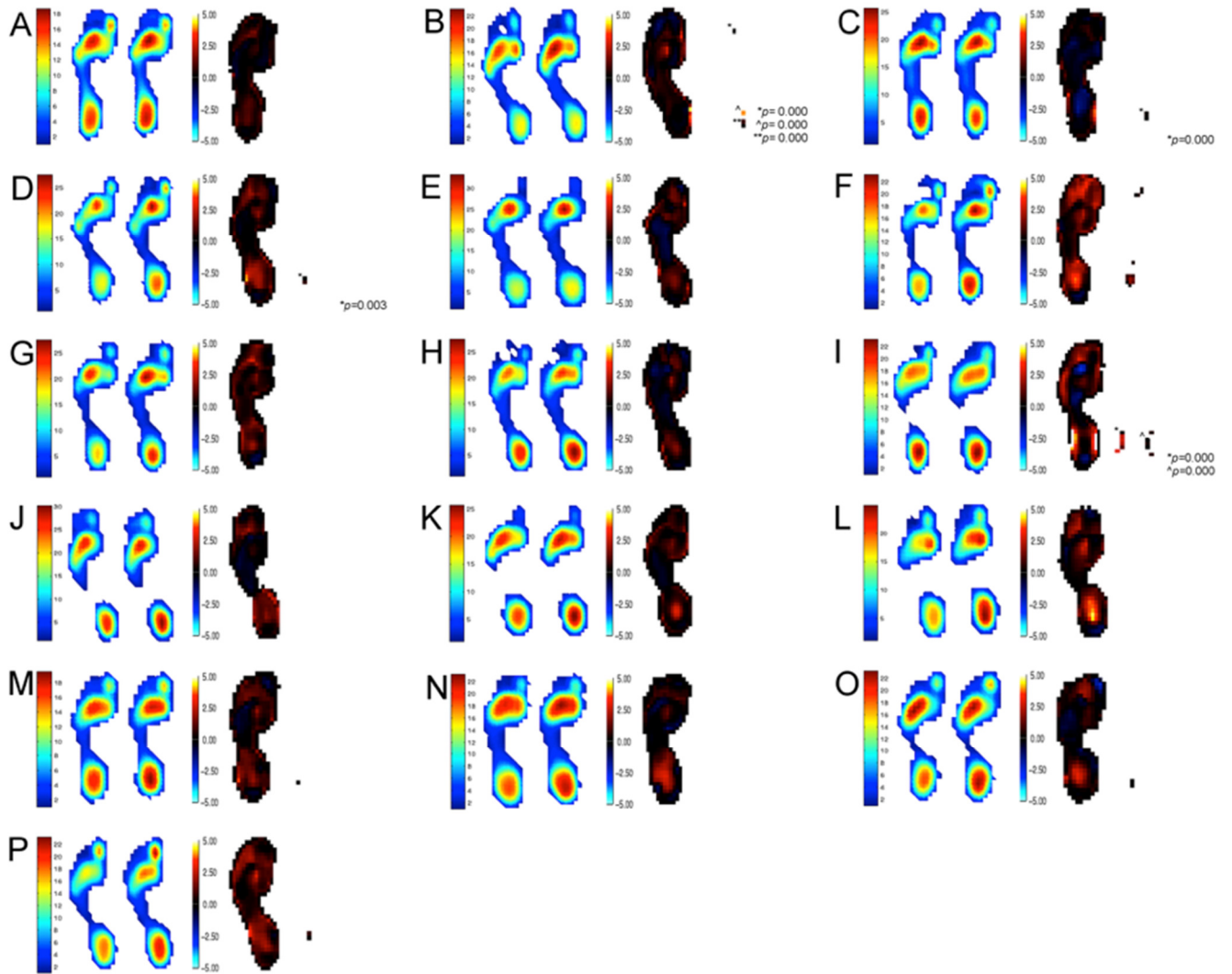


Figure S18. 1

The two left images are the mean p-images from 1.1m/s and 1. 3m/s. The centre right p-image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.1m/s and 1.3m/s trial means.

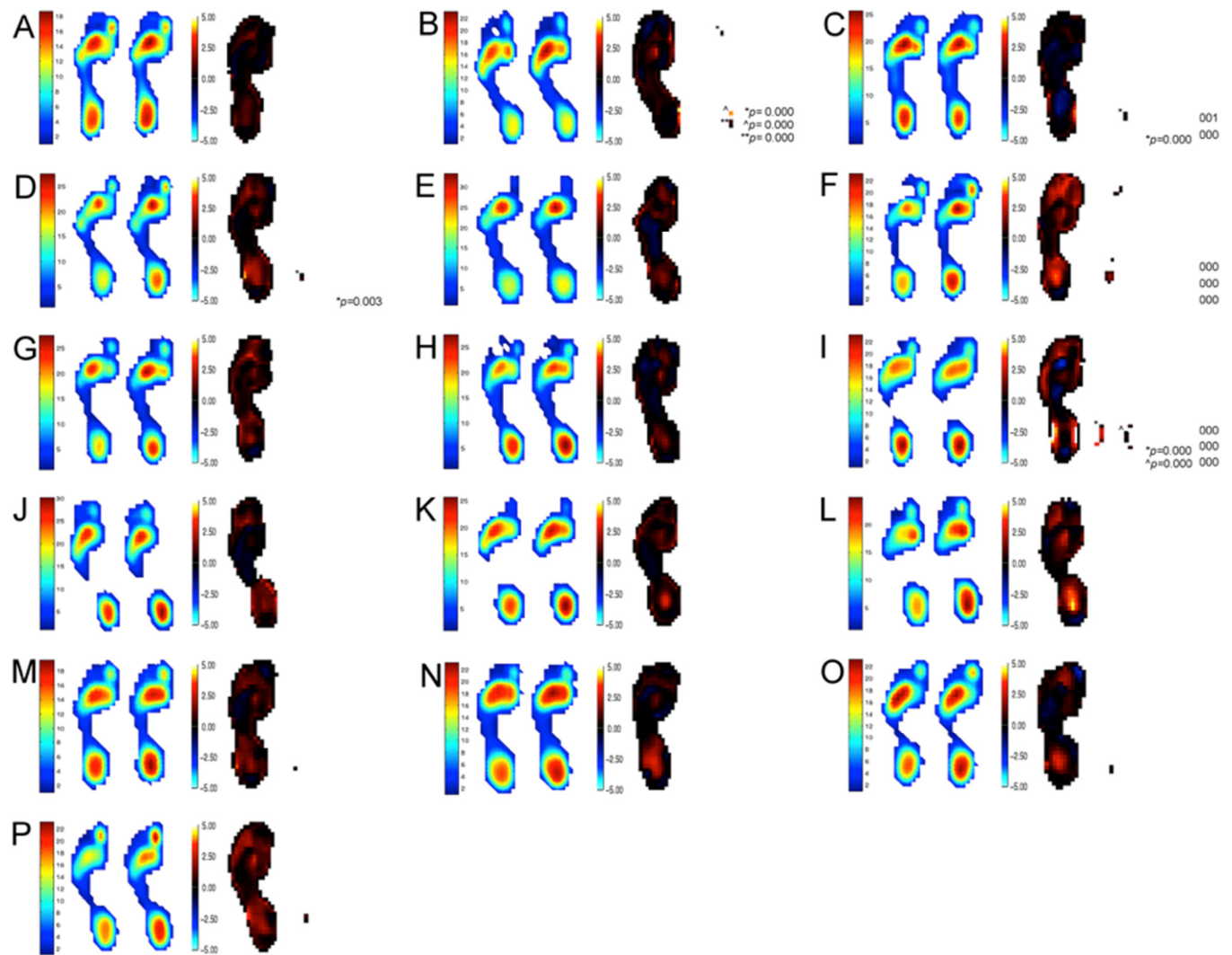


Figure S18.2

The two left images are the mean p-images from 1.1m/s and 1.5m/s. The centre right p-image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.1m/s and 1.5m/s trial means.

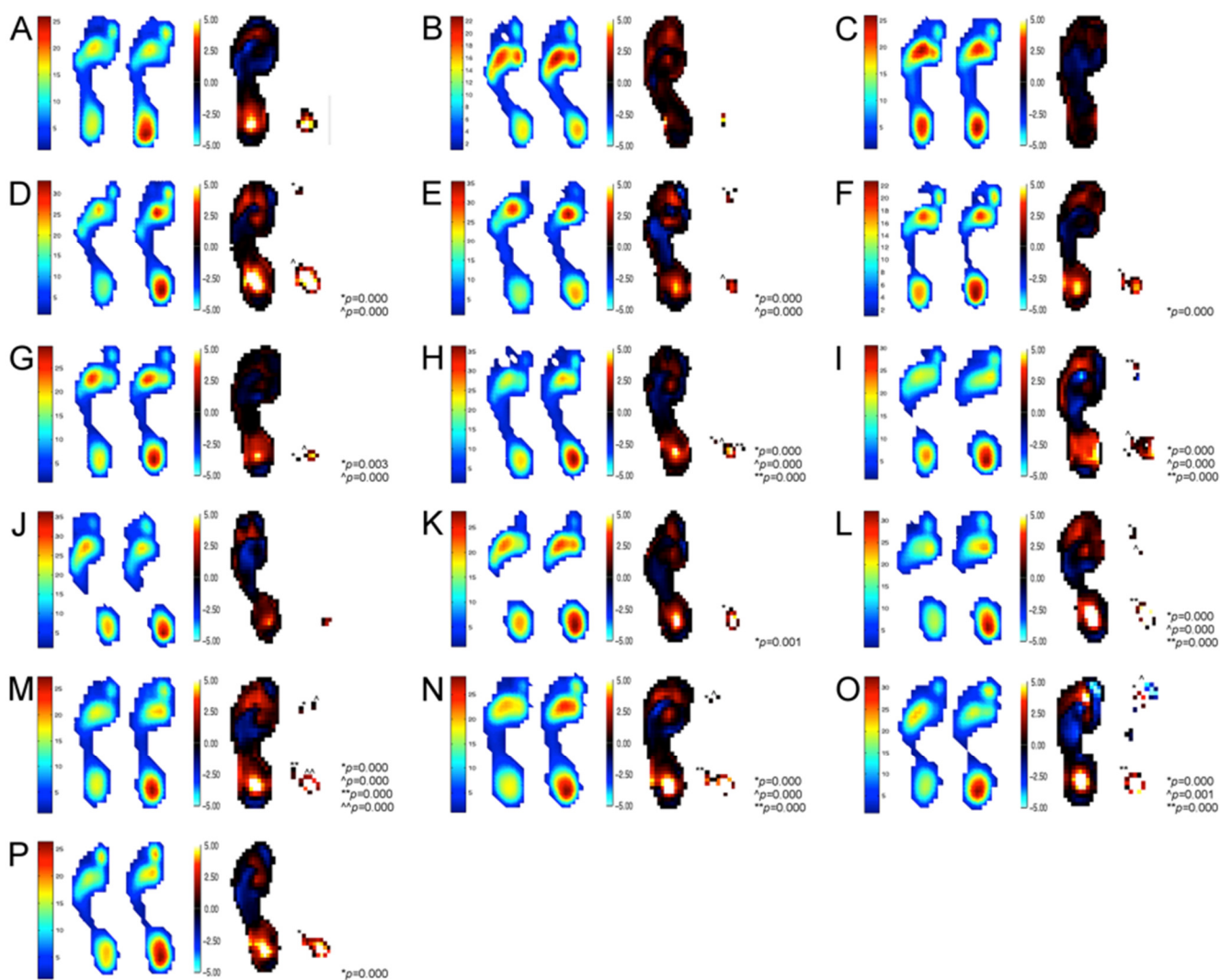


Figure S18. 3

The two left images are the mean p-images from 1.1m/s and 1.7m/s. The centre right p-image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.1m/s and 1.7m/s trial means.



Figure S18. 4

The two left images are the mean p-images from 1.1m/s and 1.9m/s. The centre right p-image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.1m/s and 1.9m/s trial means.

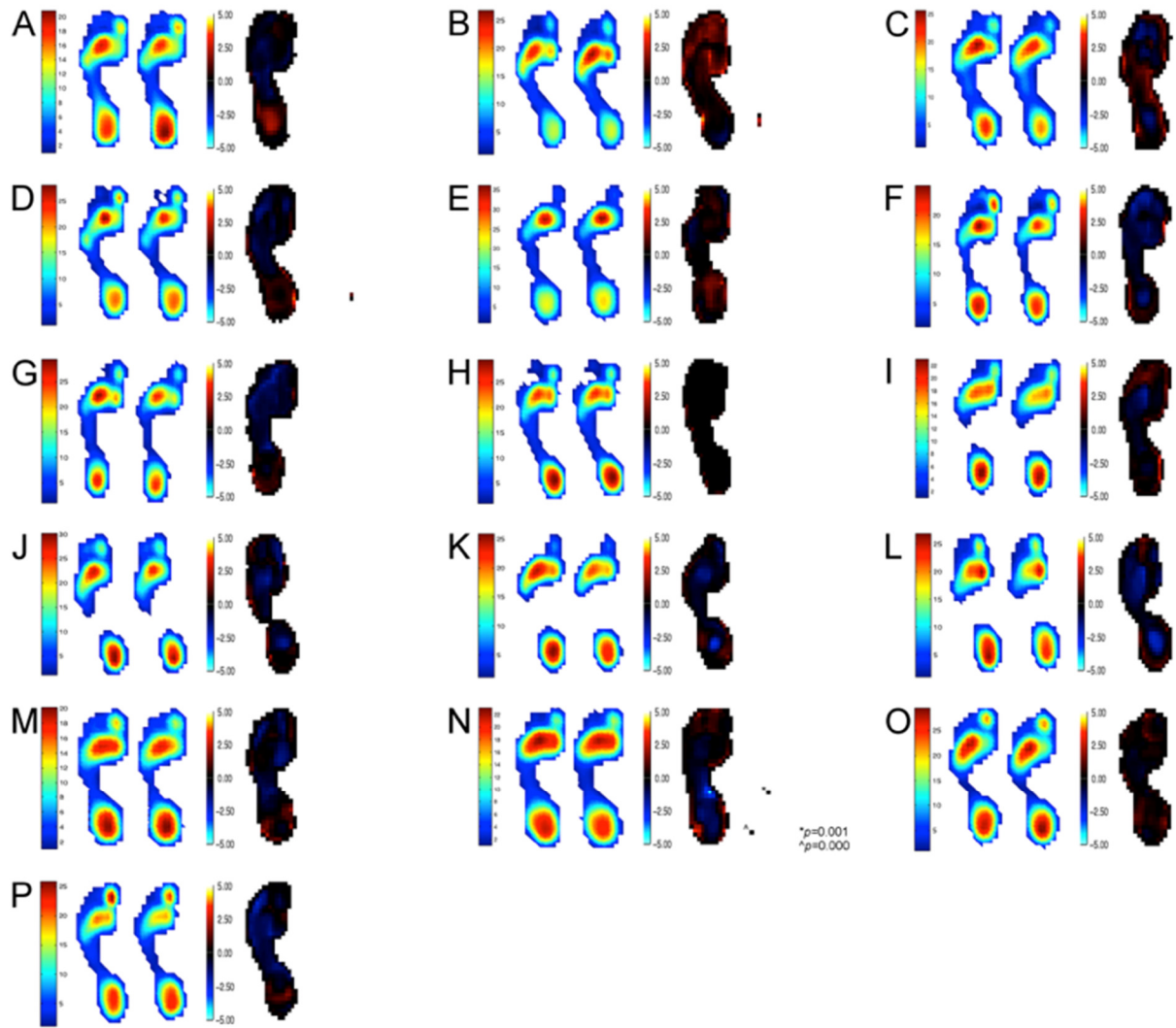


Figure S18. 5

The two left images are the mean p -images from 1.3m/s and 1.5m/s. The centre right p -image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.3m/s and 1.5m/s trial means.

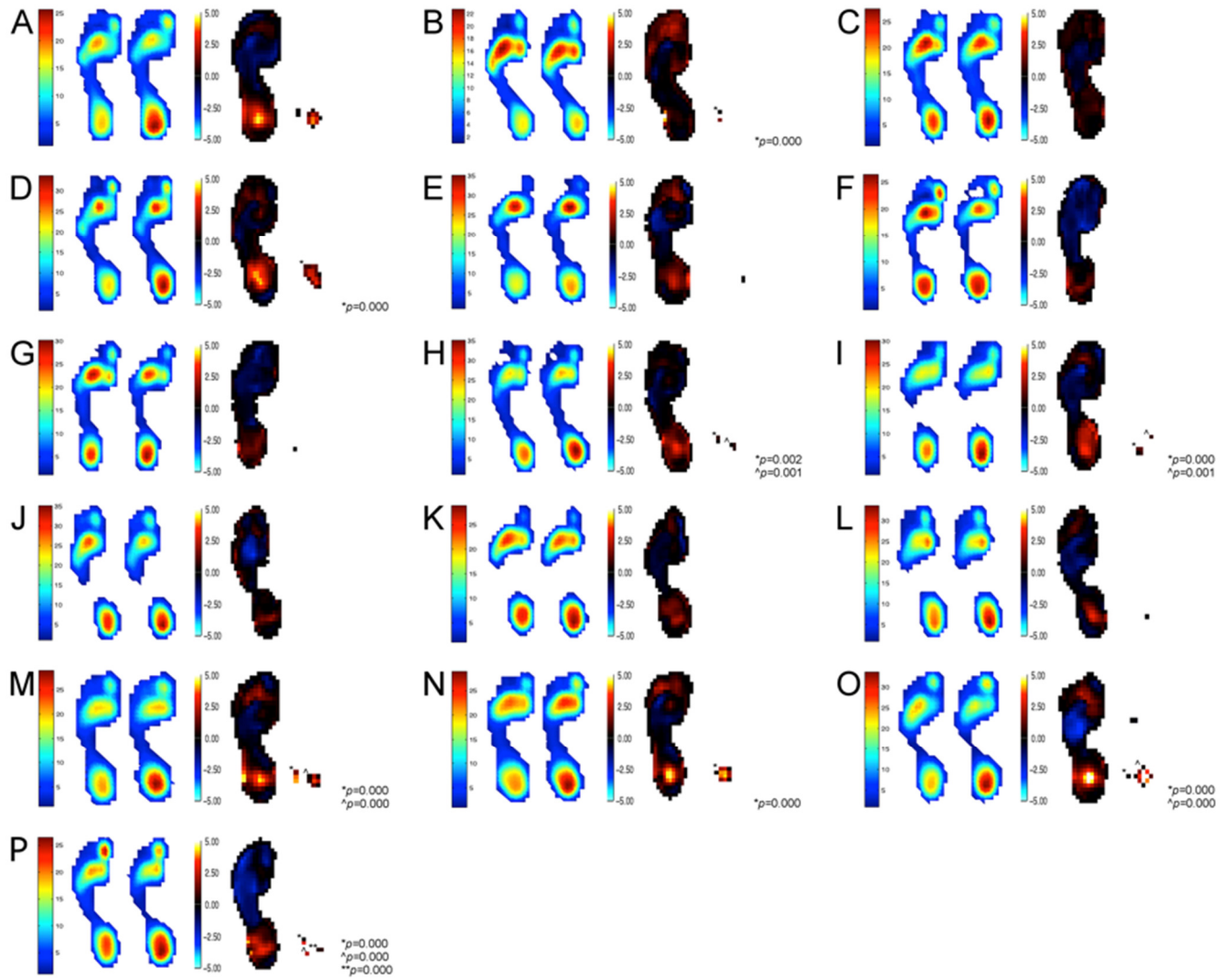


Figure S18. 6

The two left images are the mean p-images from 1.3m/s and 1.7m/s. The centre right p-image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.3m/s and 1.7m/s trial means.

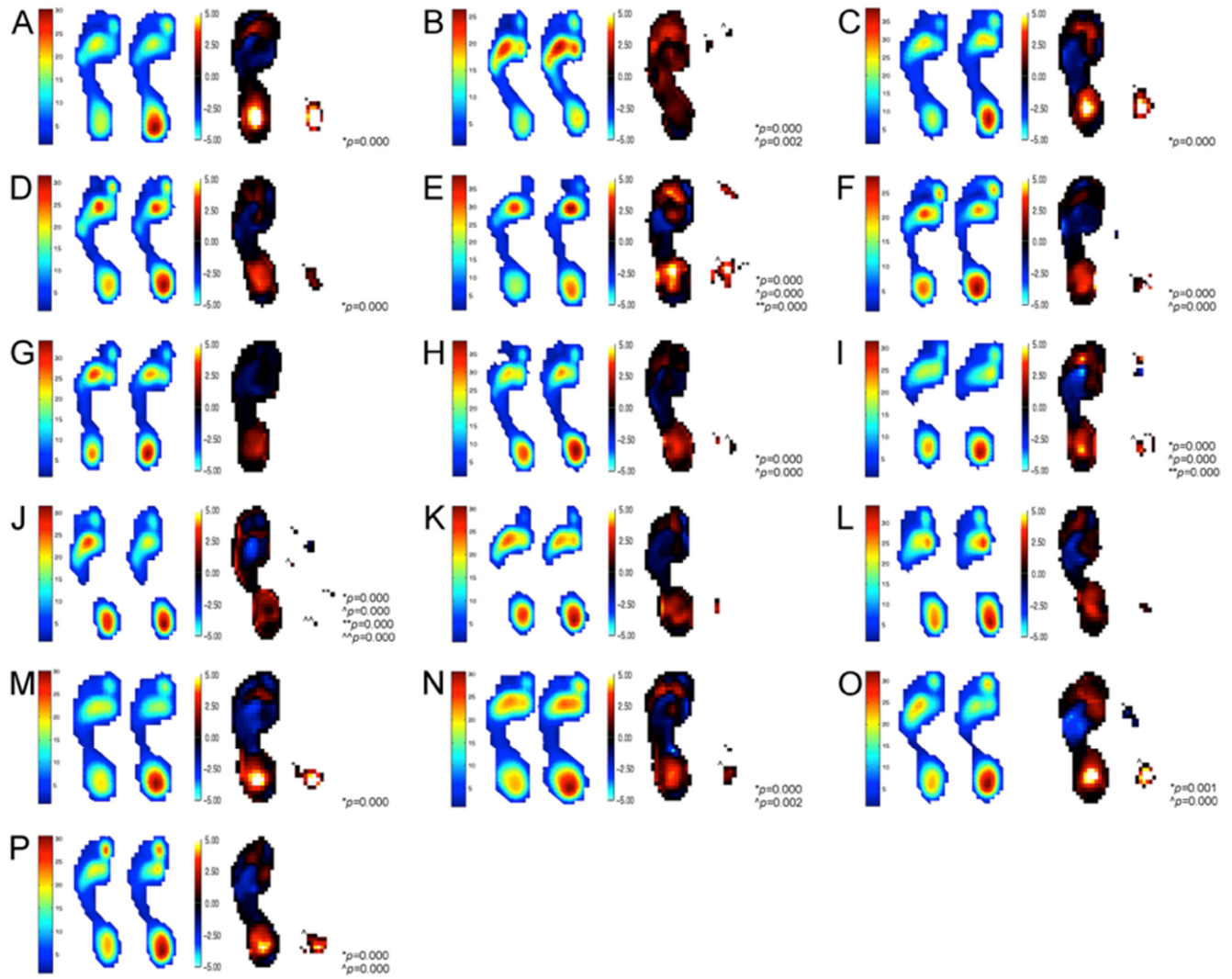


Figure S18.7

The two left images are the mean p-images from 1.3m/s and 1.9m/s. The centre right p-image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.3m/s and 1.9m/s trial means.

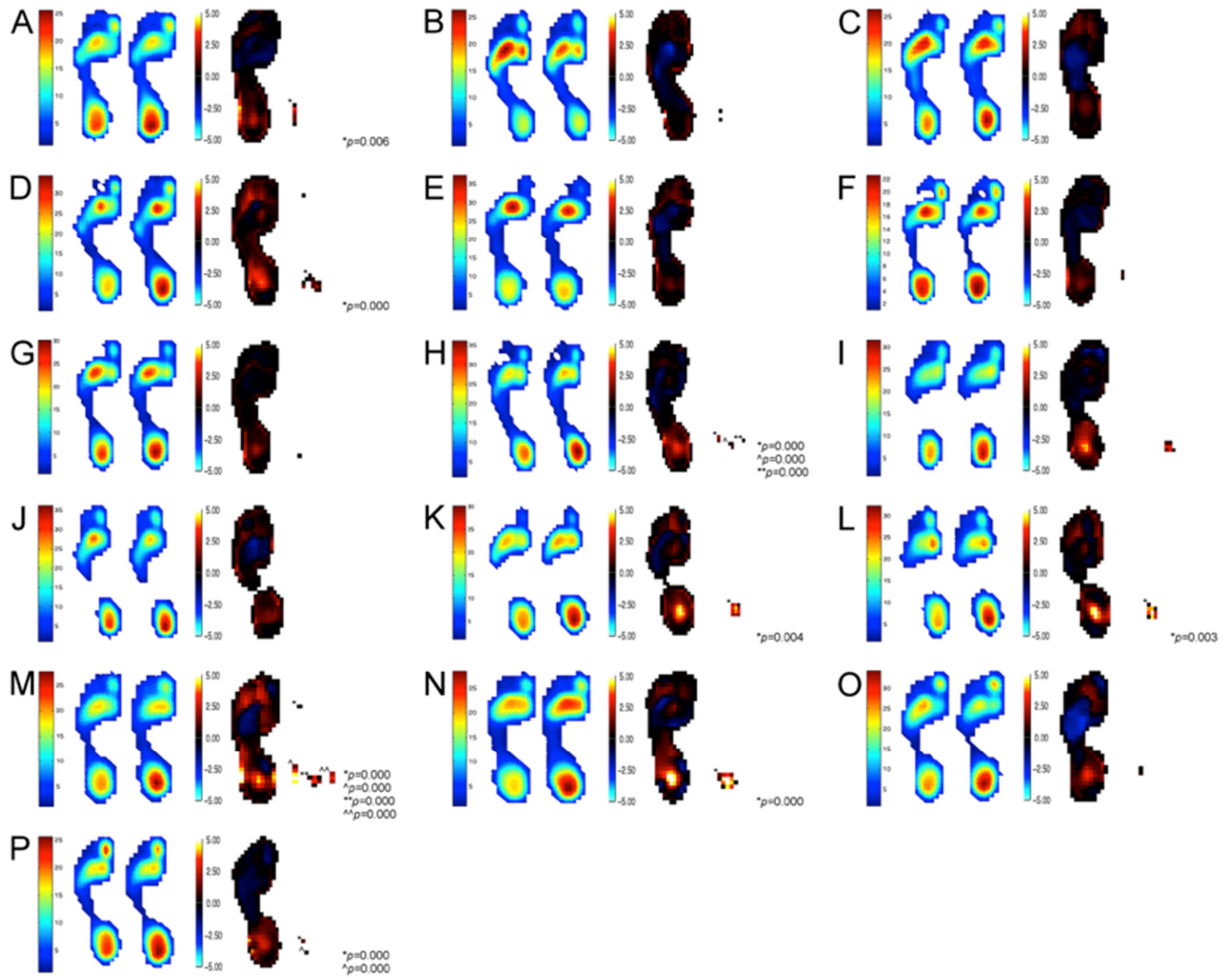


Figure S18. 8

The two left images are the mean p-images from 1.5m/s and 1.7m/s. The centre right p-image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.5m/s and 1.7m/s trial means.

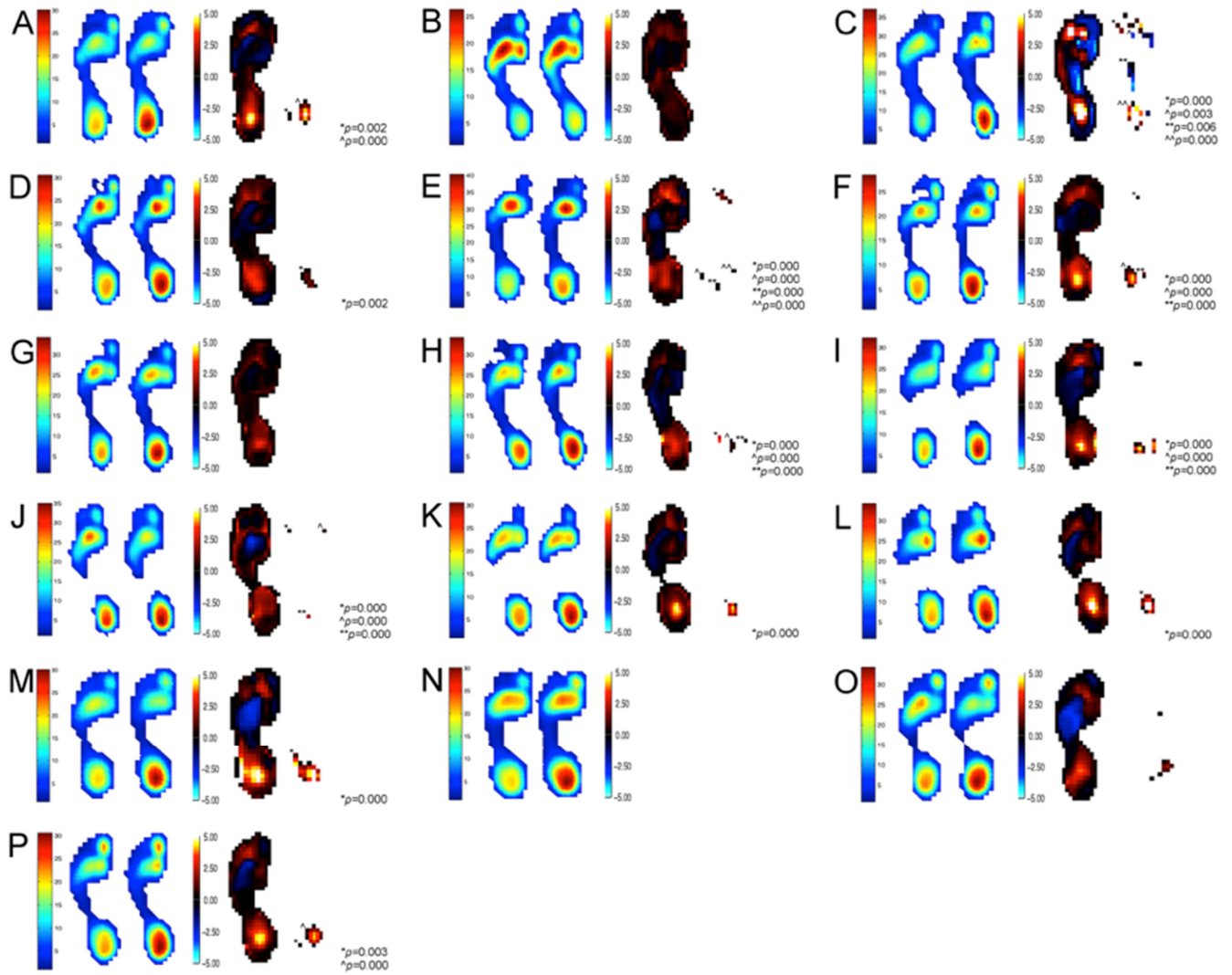


Figure S18. 9

The two left images are the mean p -images from 1.5m/s and 1.9m/s. The centre right p -image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.5m/s and 1.9m/s trial means.

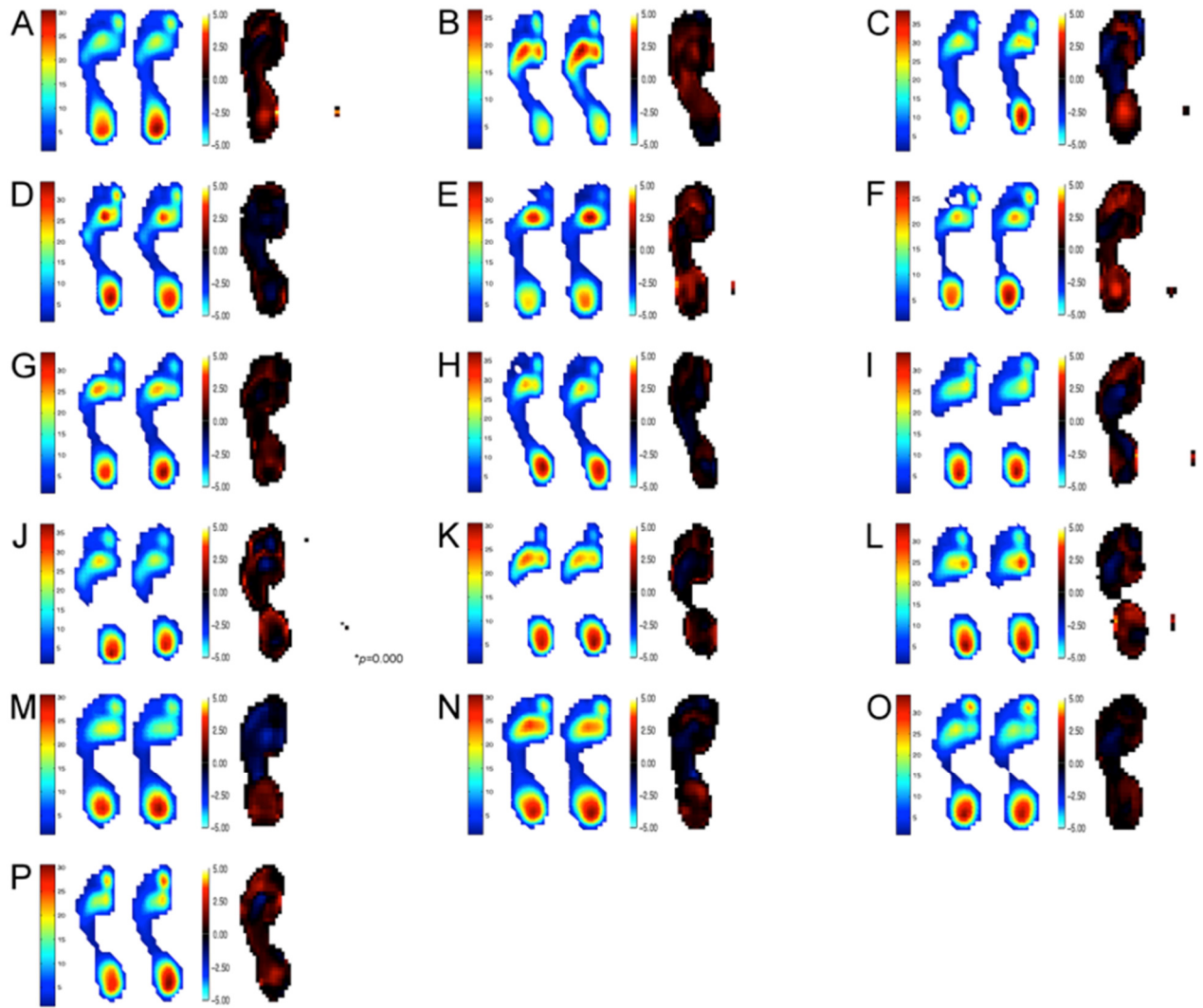
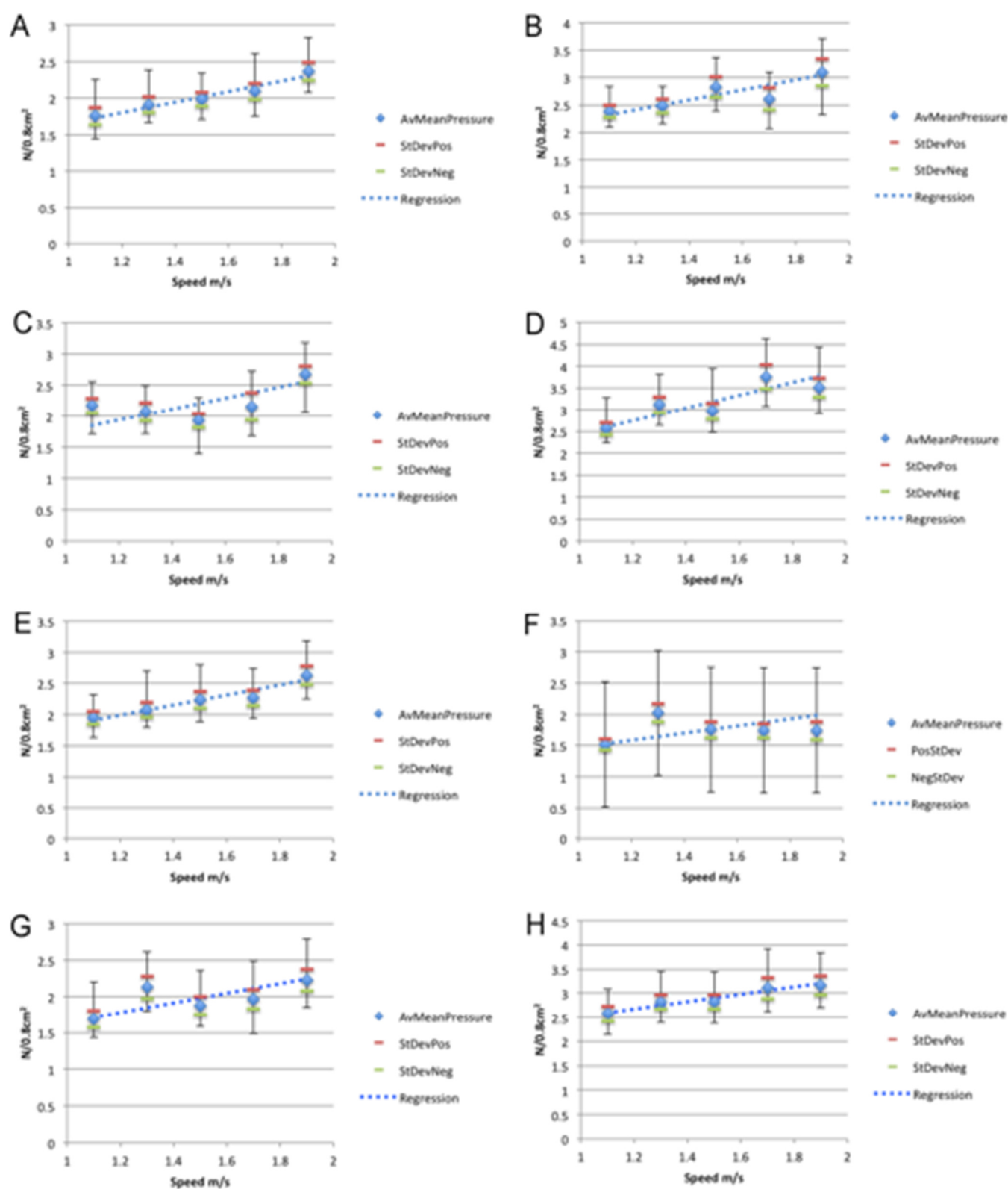


Figure S18.10

The two left images are the mean p-images from 1.7m/s and 1.9m/s. The centre right p-image is the SPM, and the far right are the probability maps, pixel clusters that represent statistically significant differences between 1.7m/s and 1.9m/s trial means.



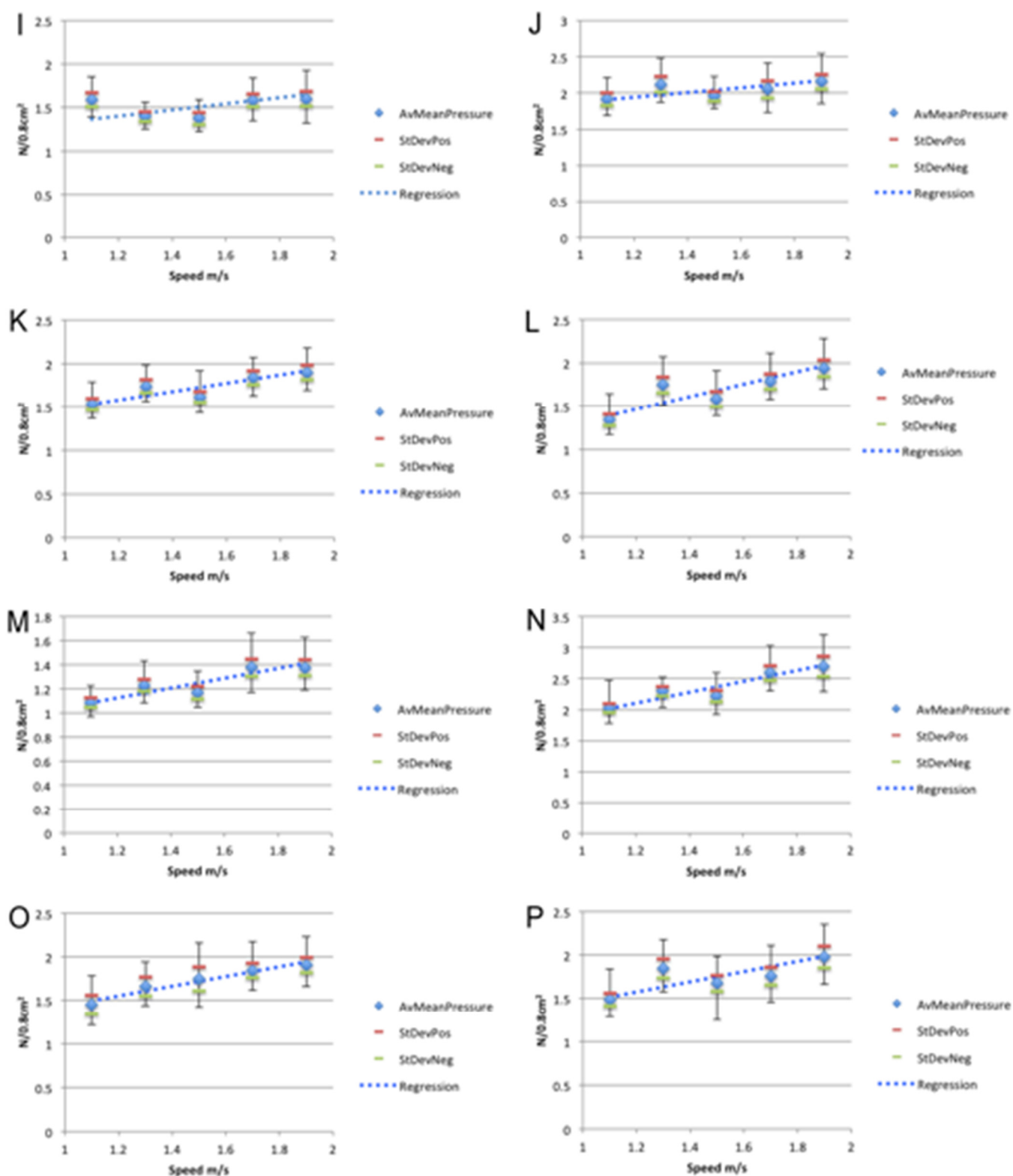
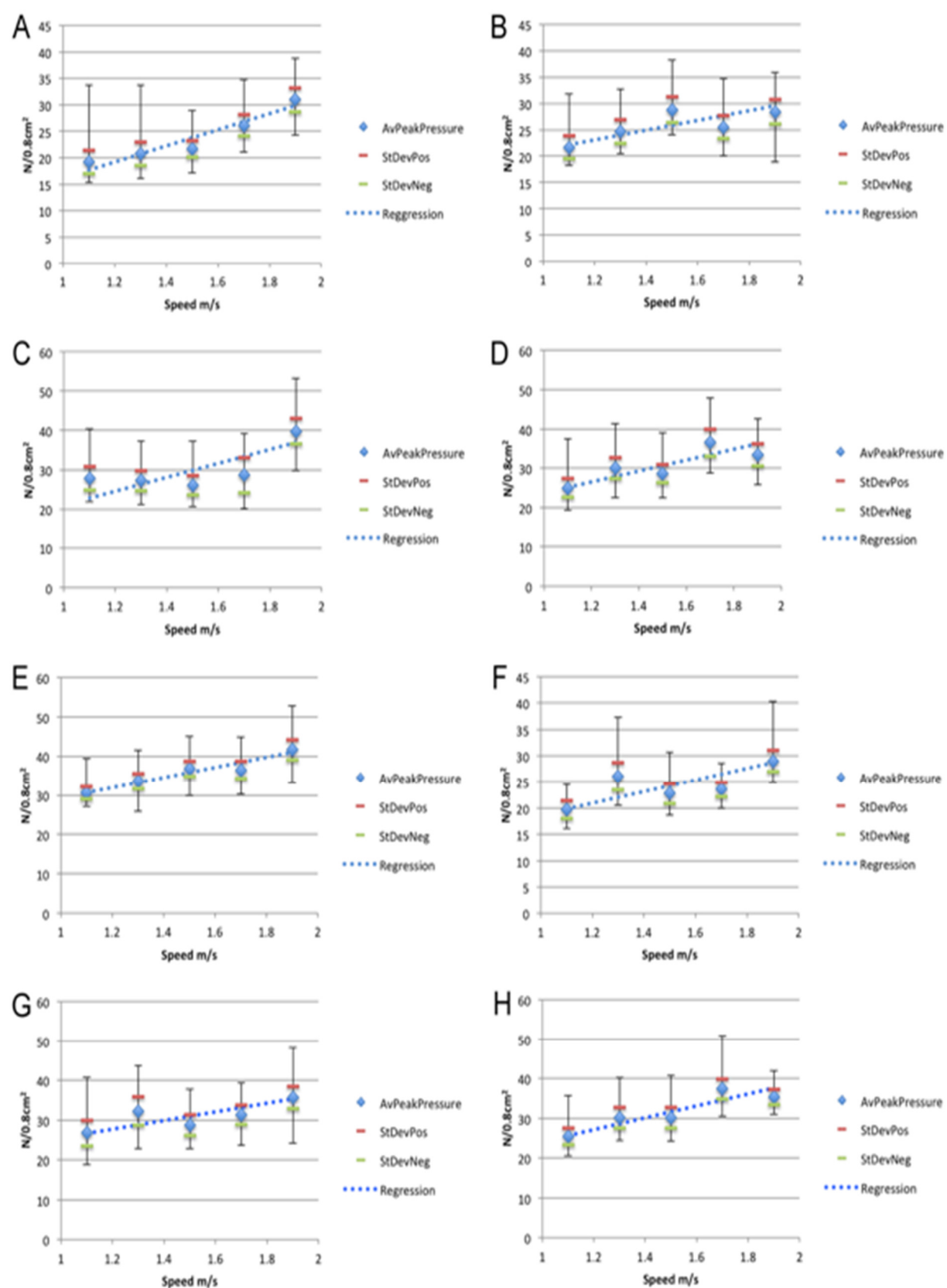


Figure S18. 11

The preceding two graphs: Discrete analysis by pSPM plots the mean, mean plantar pressure in all subjects A-P. An overall MSE (y) was calculated from the mean, registered p-image of each individual walking speed trials 1.1m/s, 1.3m/s, 1.5m/s, 1.7m/s, 1.9m/s (x) and plotted with the positive (red line) and negative (green line) standard deviations and error bars corresponding to the highest and lowest mean pressure value. RMA regression shows a general increase in average mean pressure with walking speed in all subjects.



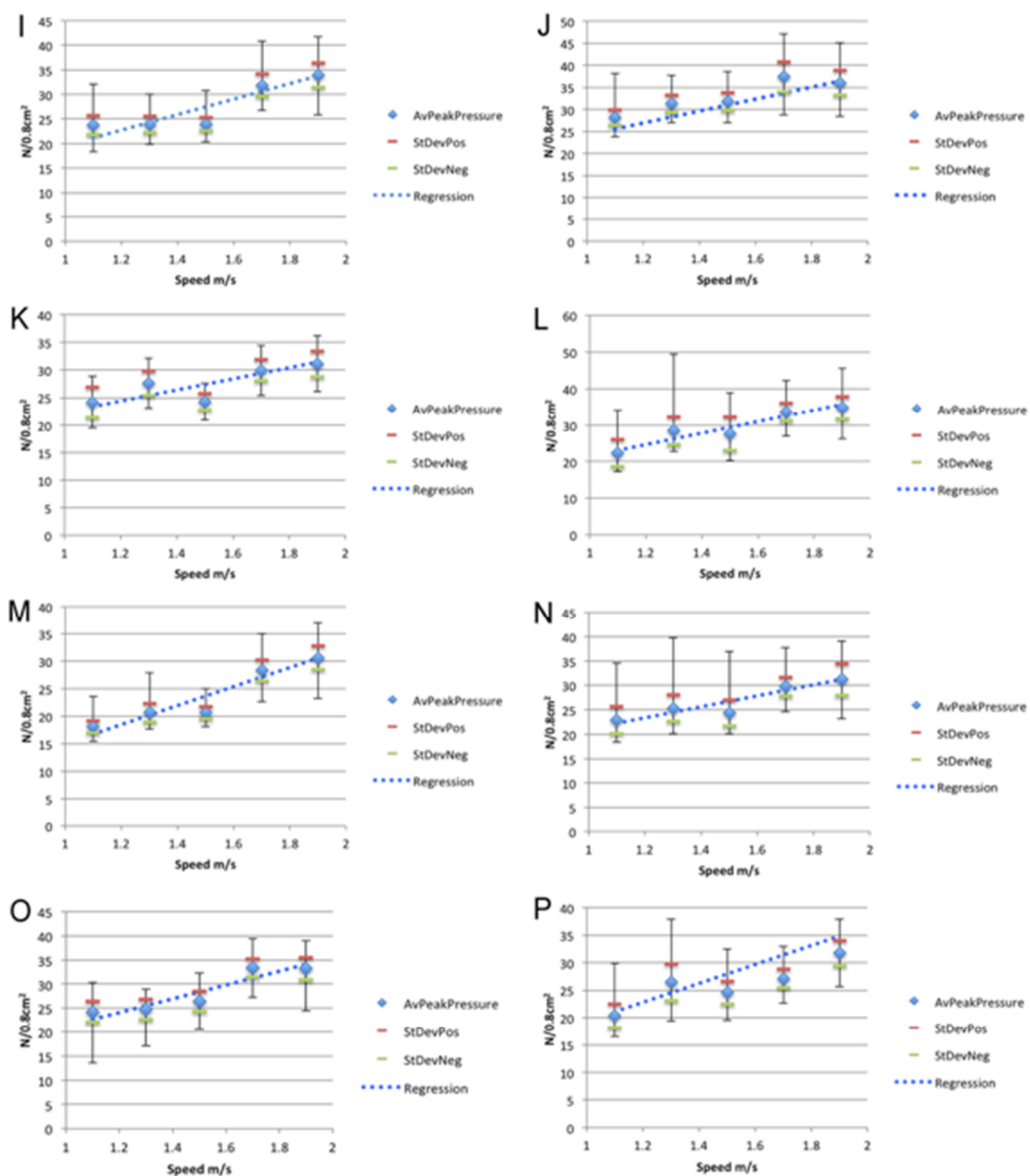
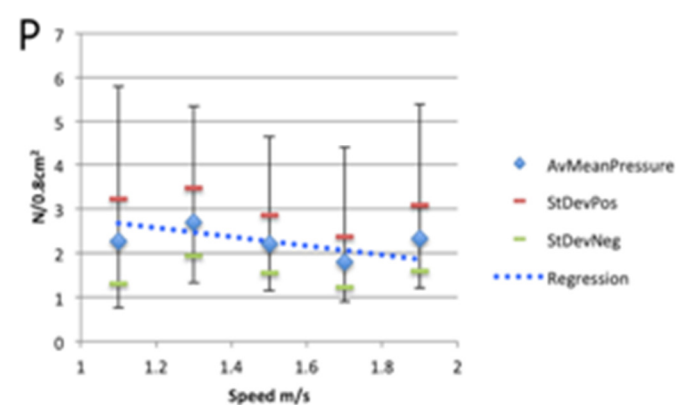
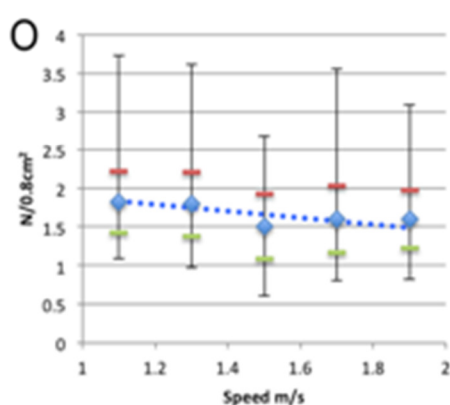
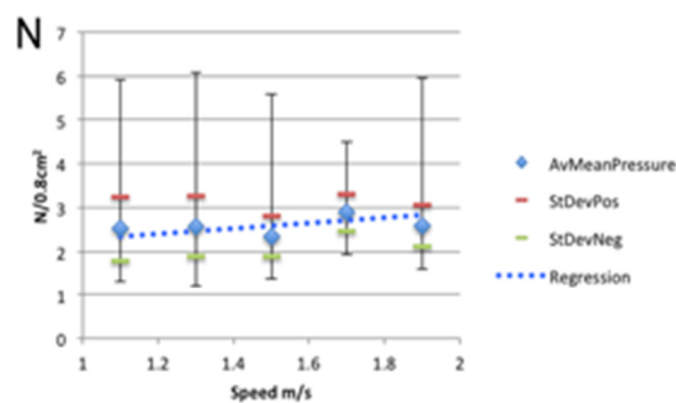
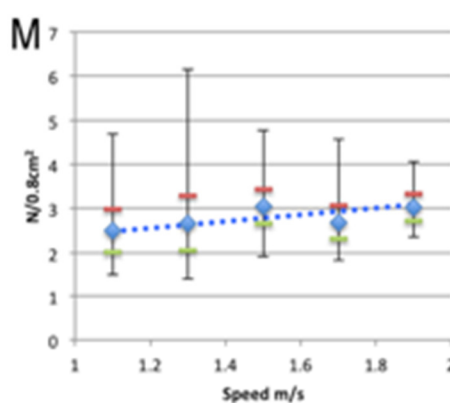
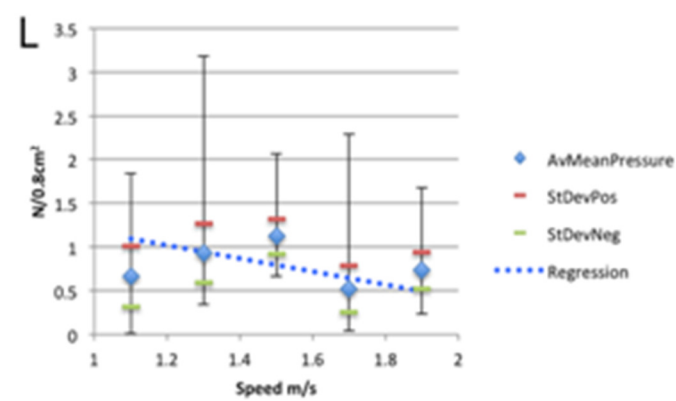
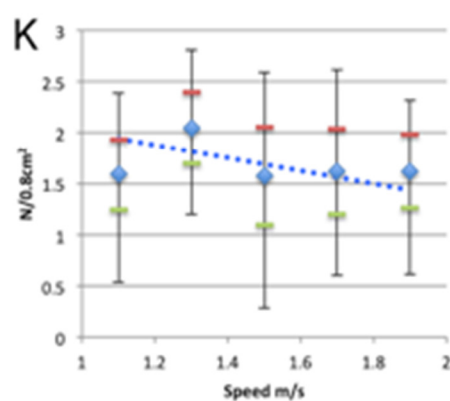
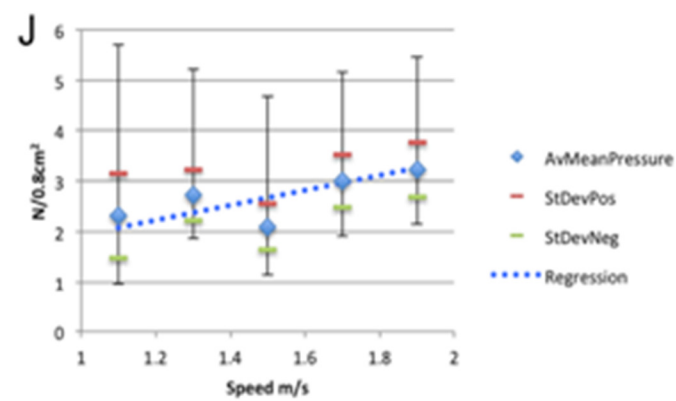
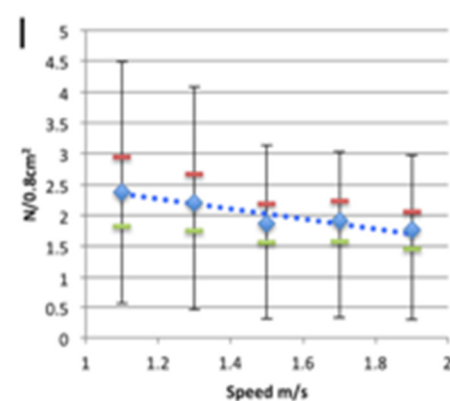


Figure S18. 12

The preceding two graphs: Discrete analysis by pSPM plots mean peak pressure in all subjects A-P. An overall mean peak pressure value (y) was calculated from the mean, registered p-image of each individual walking speed trial 1.1m/s, 1.3m/s, 1.5m/s, 1.7m/s, 1.9m/s (x) and plotted with the positive (red line) and negative (green line) standard deviations and error bars corresponding to the highest and lowest peak pressure value. RMA regression shows a general increase in average peak pressure with walking speed in all subjects.



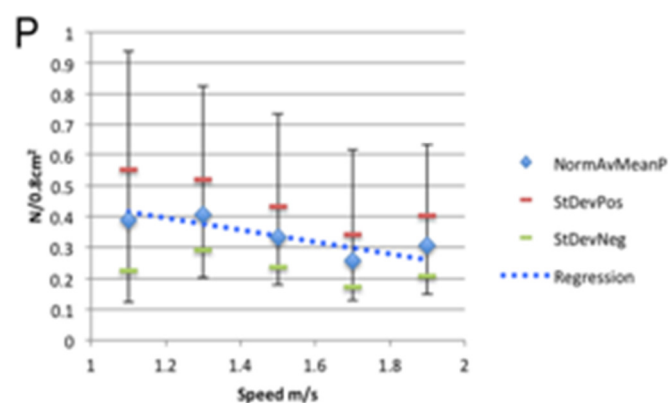
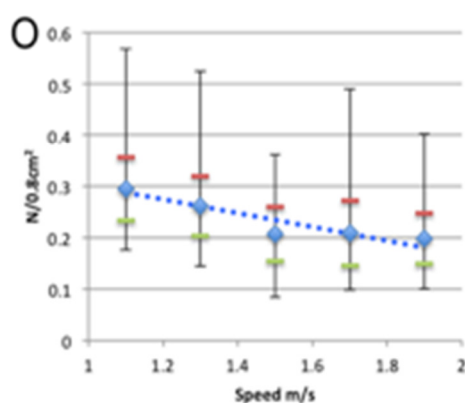
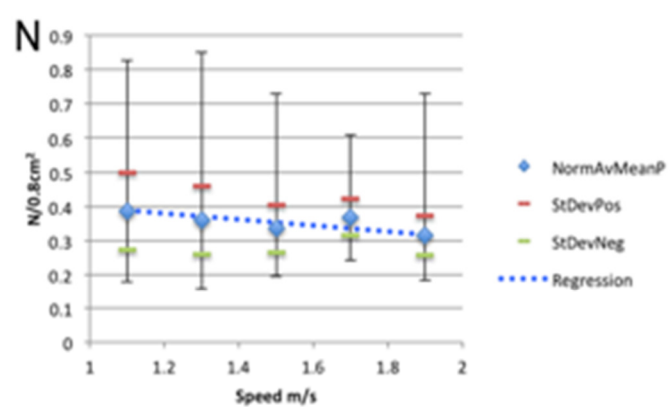
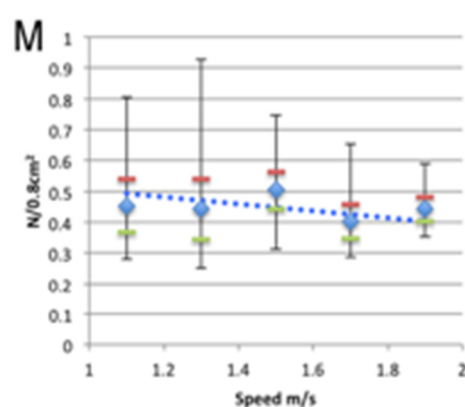
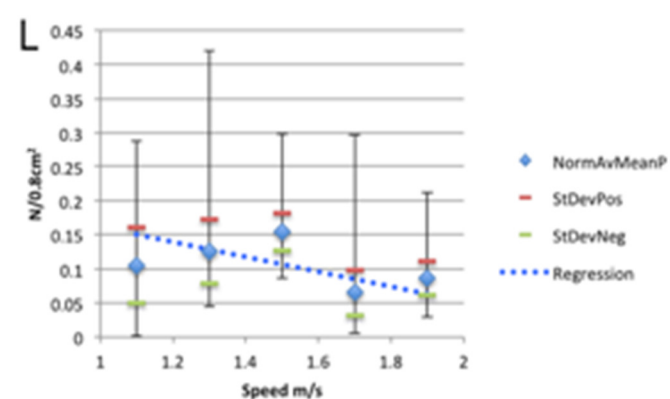
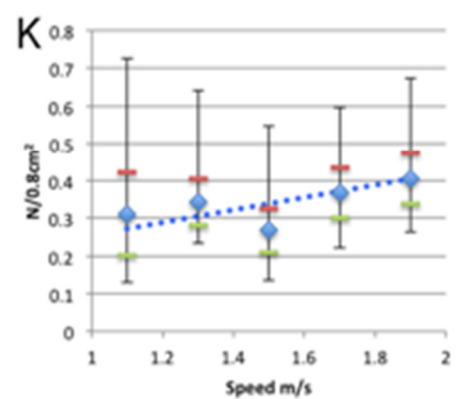
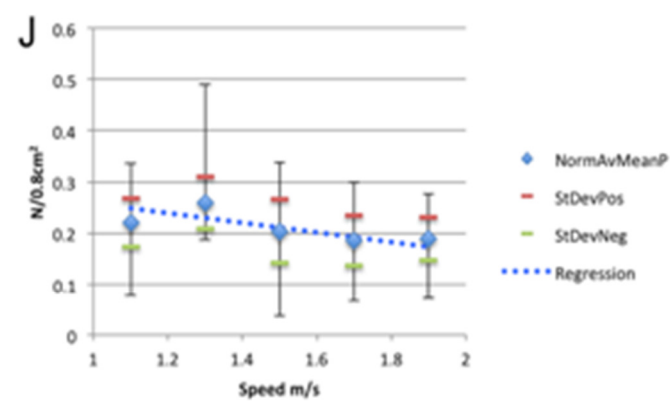
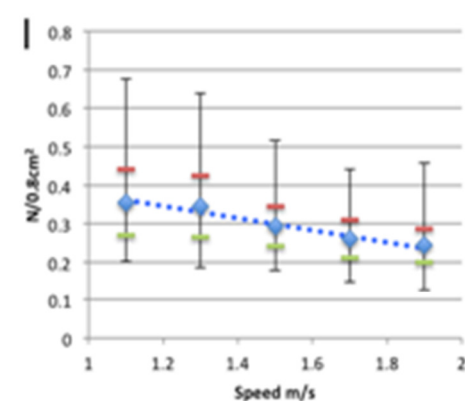
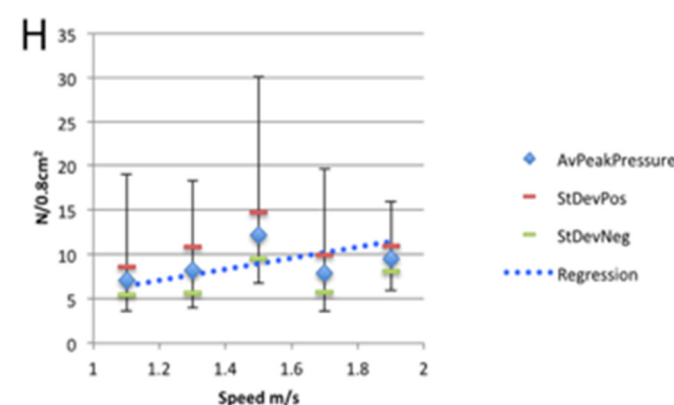
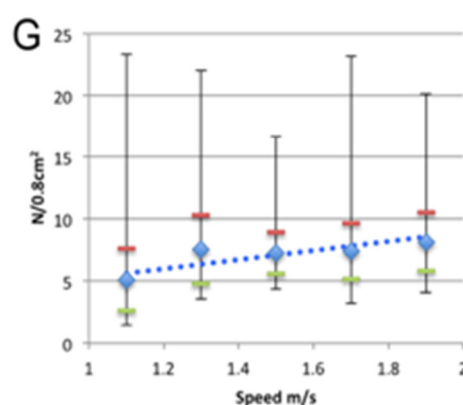
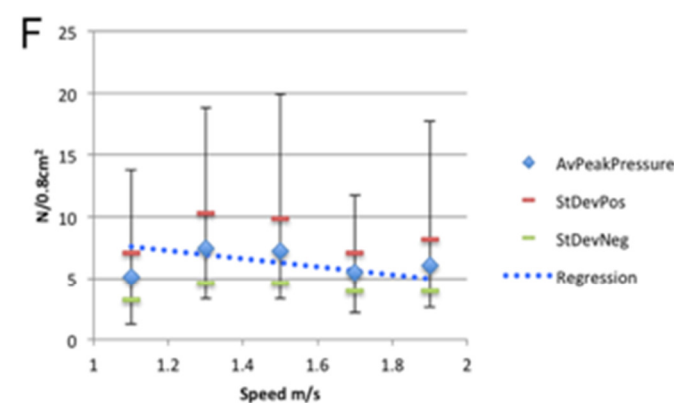
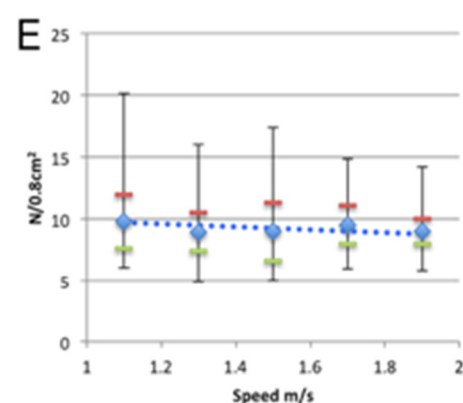
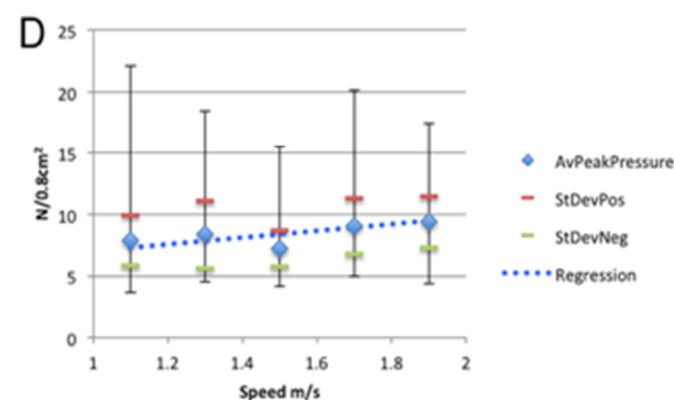
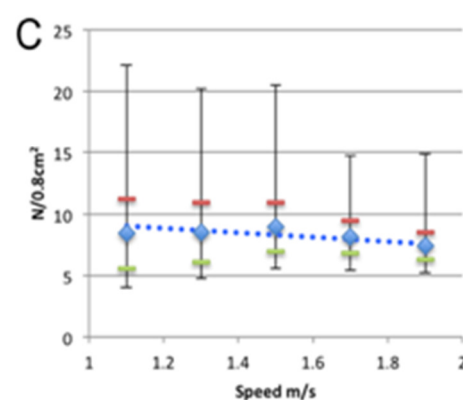
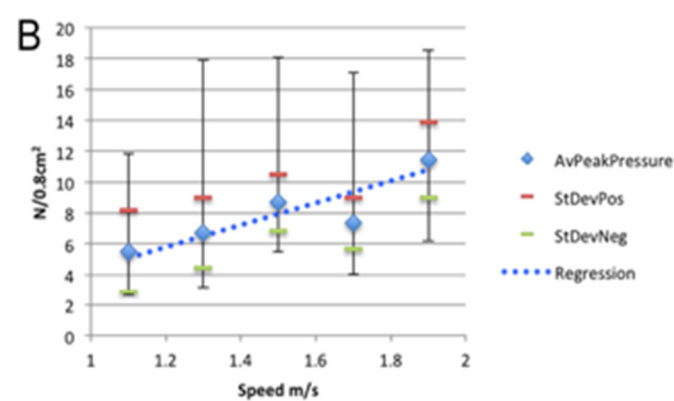
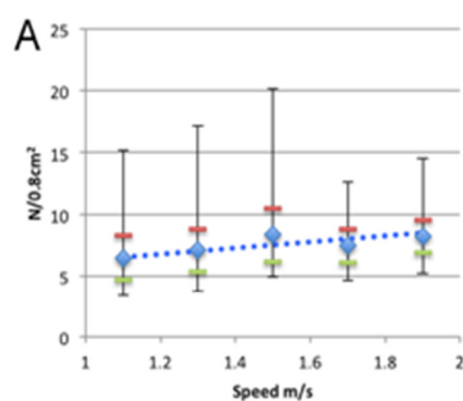


Figure S18. 13

The preceding two graphs: Discrete analysis by pSPM of the mean, mean midfoot pressure in all subjects A-P. An overall mean pressure value (y) was calculated from the mean, registered p-image of each individual walking speed trial 1.1m/s, 1.3m/s, 1.5m/s, 1.7m/s, 1.9m/s (x) and plotted with the positive (red line) and negative (green line) standard deviations and error bars corresponding to the highest and lowest mean midfoot pressure value. RMA regression shows a general increase in the mean, mean midfoot pressure with walking speed in most subjects.



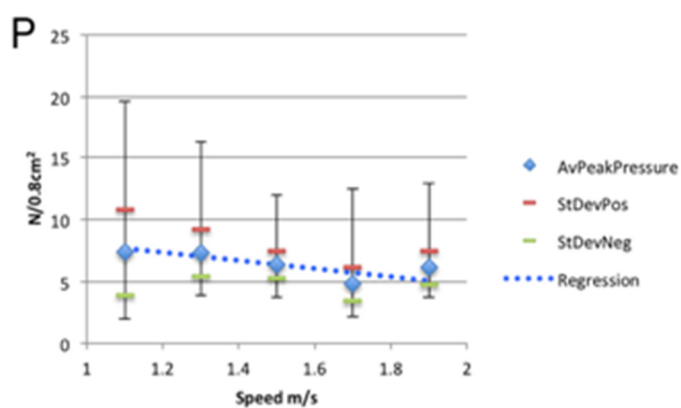
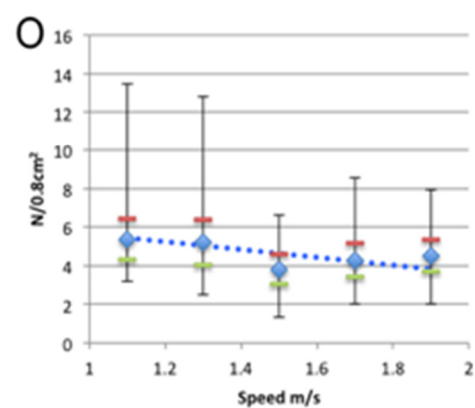
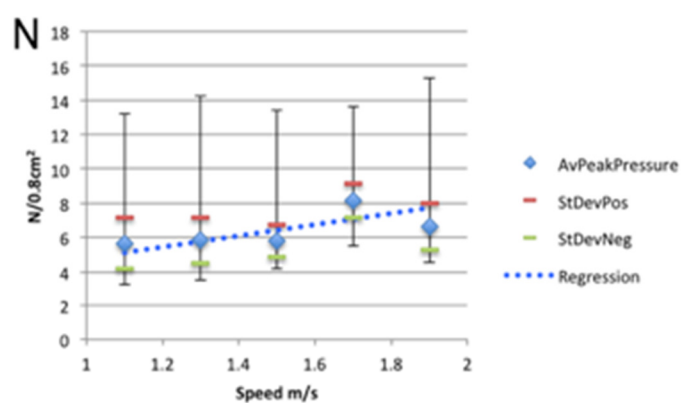
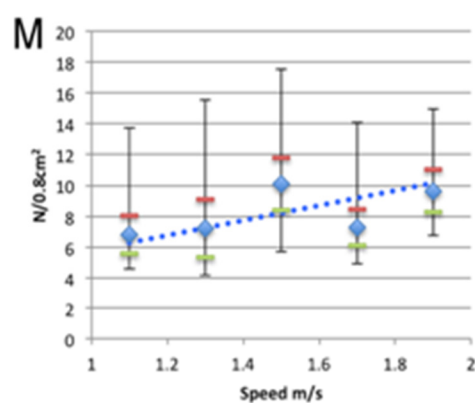
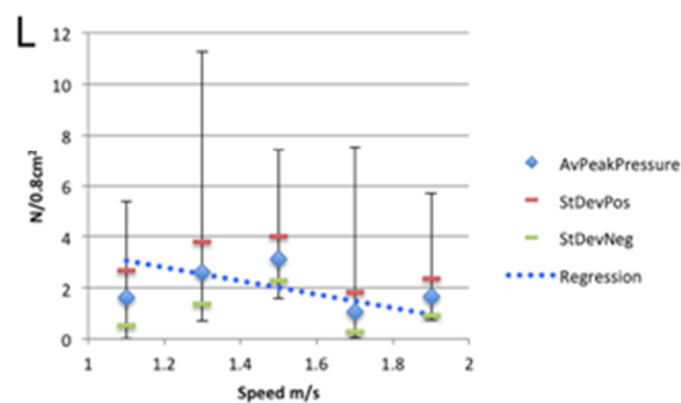
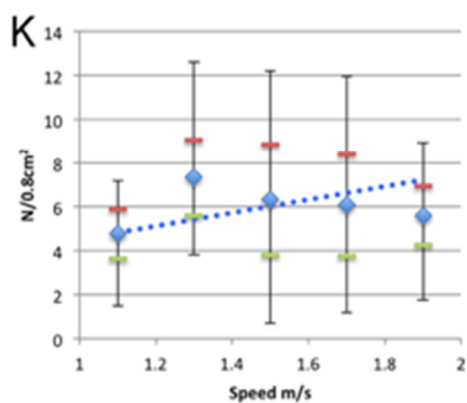
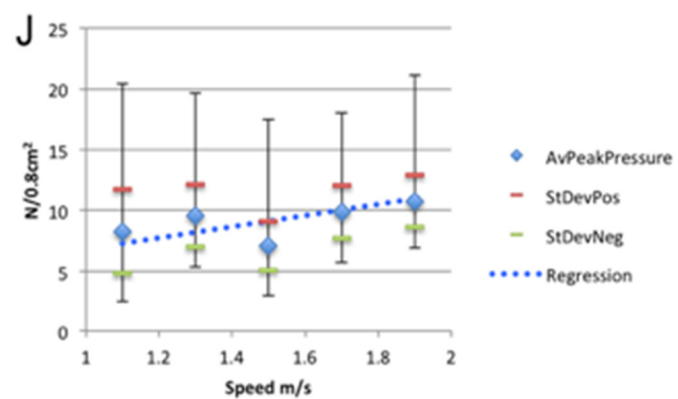
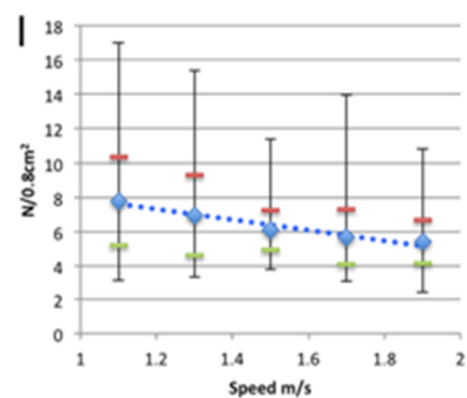
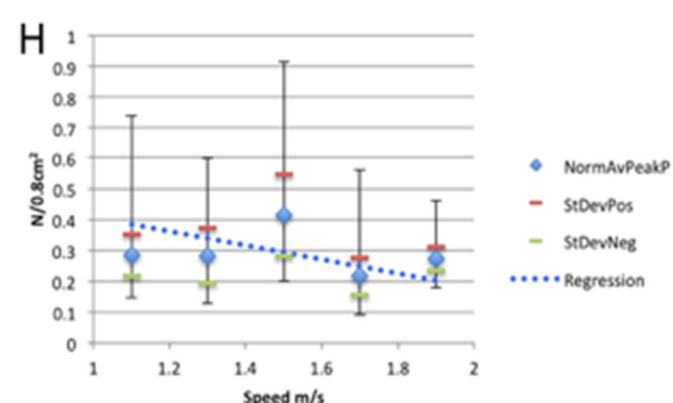
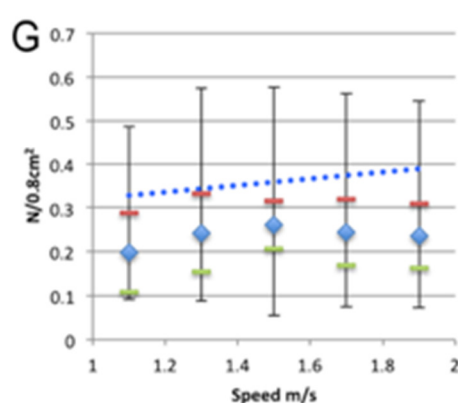
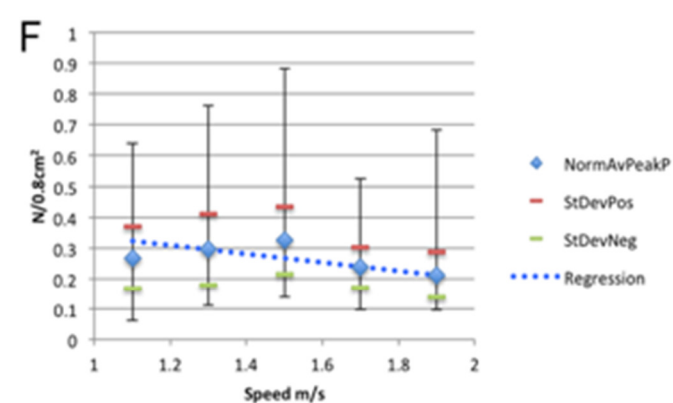
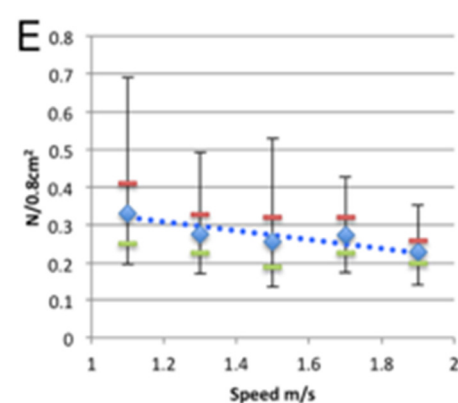
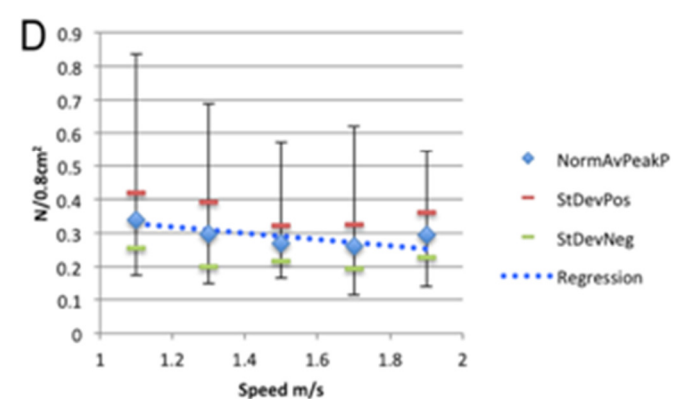
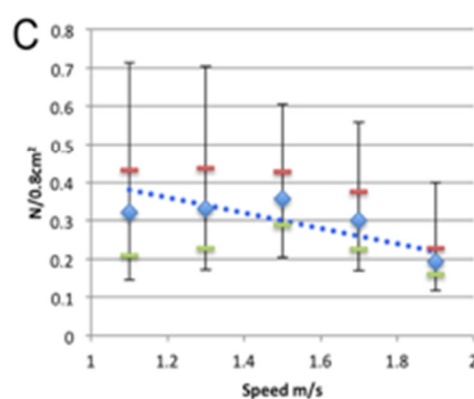
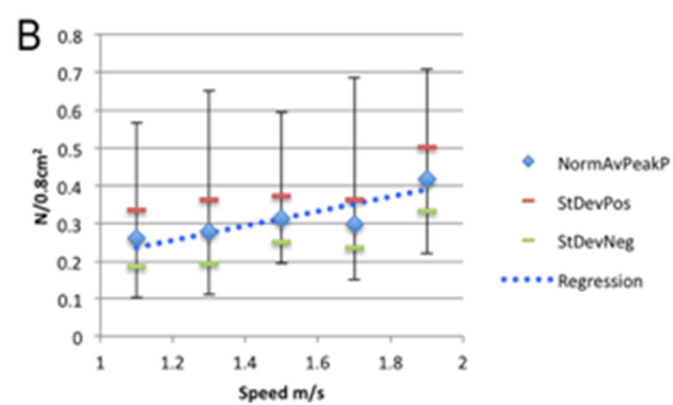
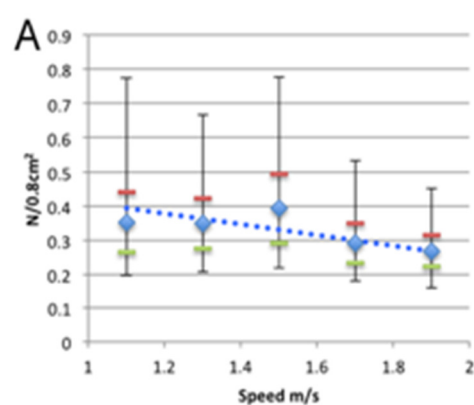


Figure S18. 14

The preceding two graphs: Discrete analysis by pSPM of the normalised average mean midfoot pressure in subjects A-P and all walking speeds tested from 1.1-1.9m/s. Positive and negative standard deviations above (red line) and below (green line), with error bars corresponding to the highest and lowest normalised mean midfoot pressure for a single footfall at each speed. RMA regression reports decreasing mean peak midfoot pressure with speed in 13 of the 16 subjects.



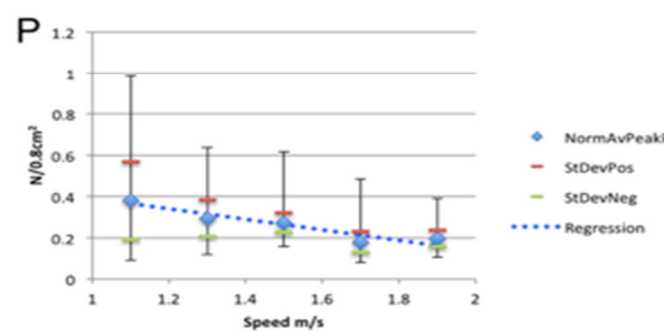
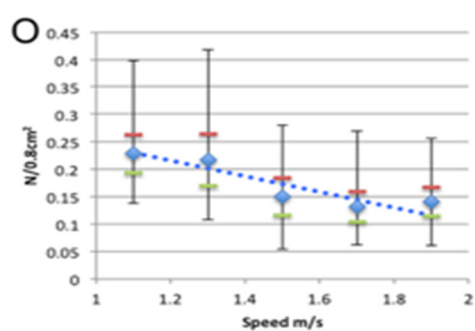
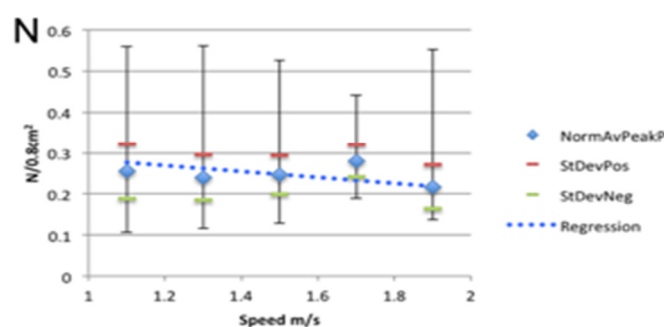
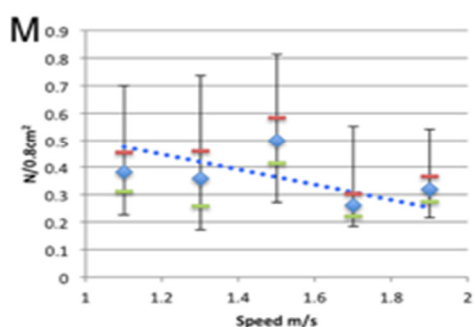
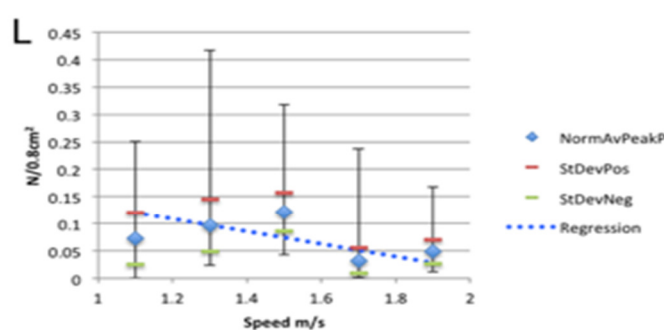
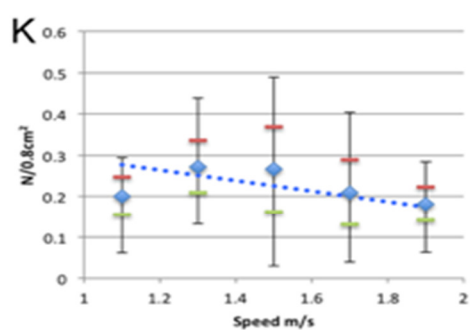
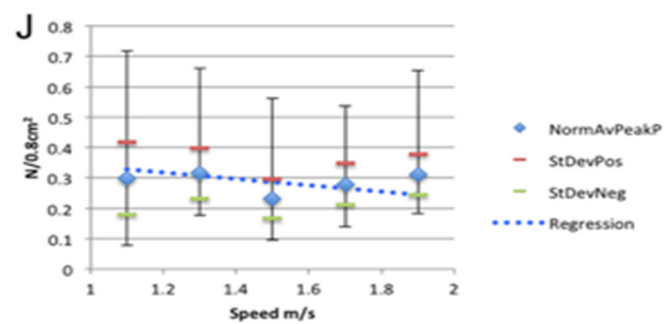
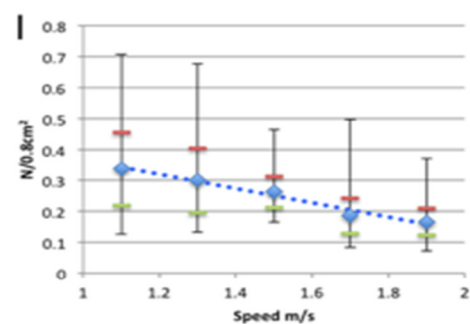


Figure S18. 15

The preceding two graphs: Discrete analysis by pSPM of the normalised Relation between the normalised average mean midfoot pressure in subjects A-P and all walking speeds tested from 1.1-1.9m/s. Positive and negative standard deviations above (red line) and below (green line), with error bars corresponding to the highest and lowest normalised mean midfoot pressure for a single footfall at each speed. RMA regression reports decreasing mean peak midfoot pressure with speed in 13 of the 16 subjects.

23.2 Chapter 19 supplementary materials

The following chapter represents the figures produced from each pressure vs. speed comparison made at all speeds across all subjects in chapter 19. Figures depict the exponential relationship between the range in the MSE of larger sample sizes when assessed by random subsampling. The following includes all tests at all speeds.

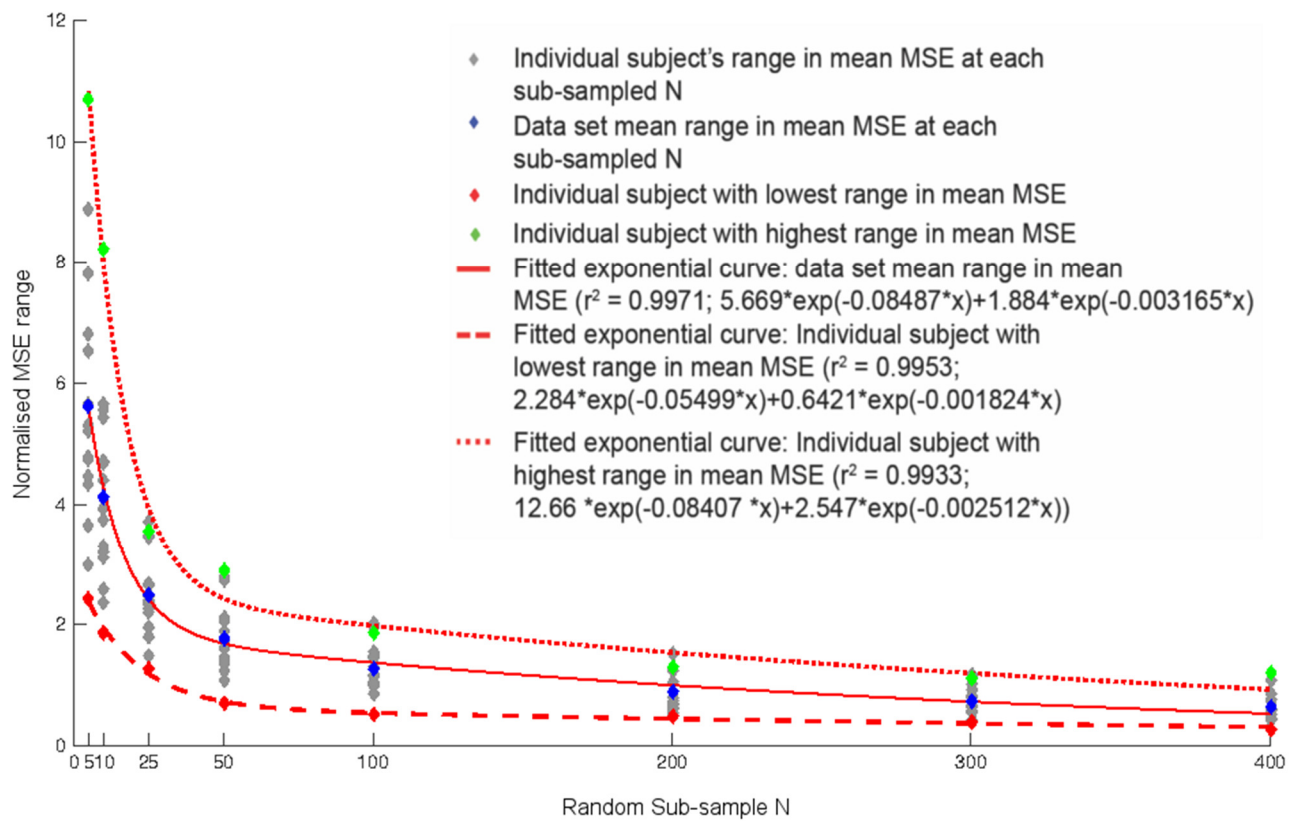


Figure S19. 1

The relationship between individual trial n and the sensitivity of the MSE at randomly generated subsamples ($n = 5, 10, 25, 50, 100, 200, 300, 400$), re-generated 1000 times per sub-sample at 1.1m/s. Exponential curves describe this relationship well in all subjects. This relationship is observed here: combined mean of all 16 subjects (solid curve), individual walking speed trial mean of subjects with the highest (subject G, dotted curve) and lowest (subject M, dashed curve) overall MSE.

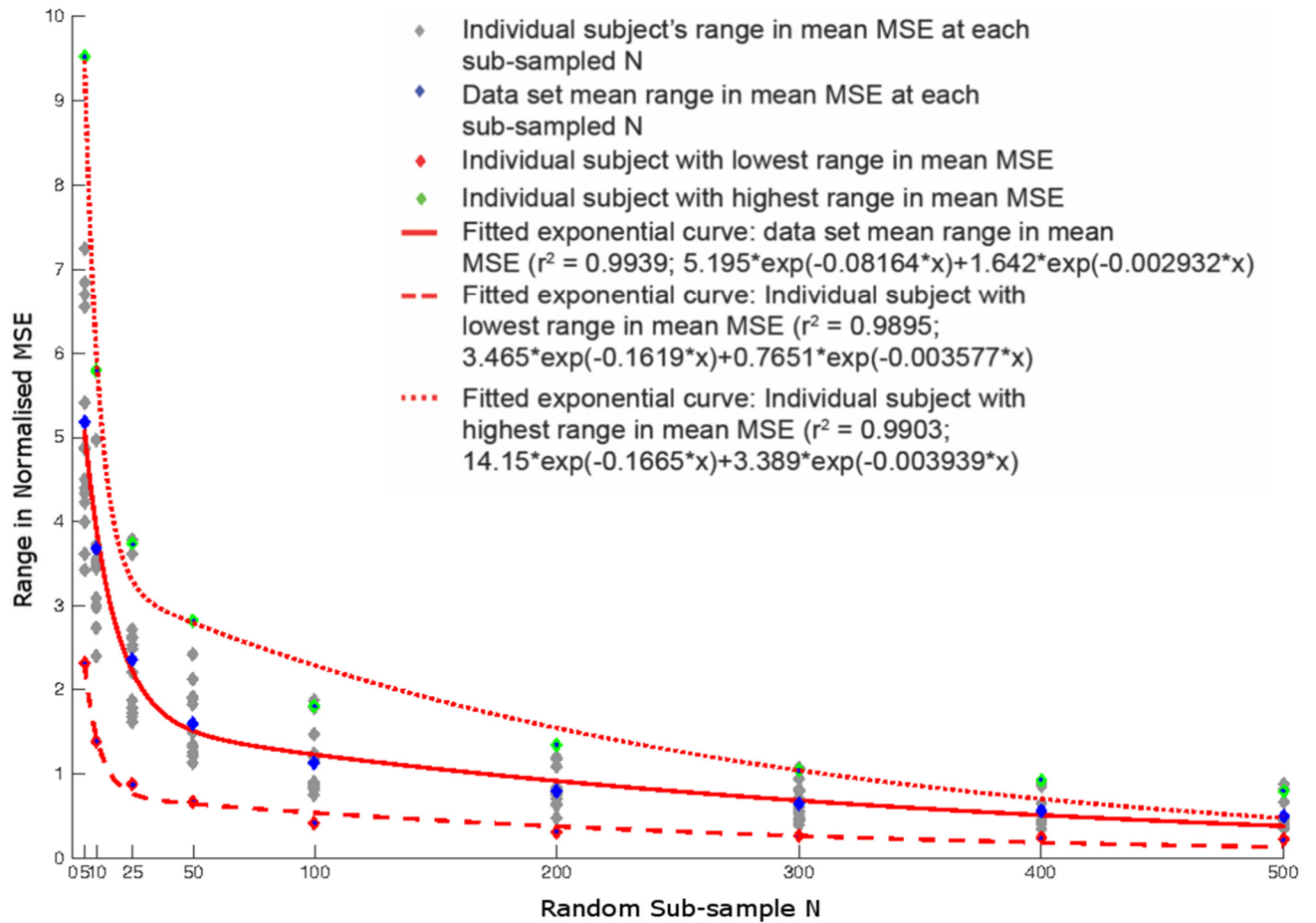


Figure S19. 2

The relationship between individual trial n and the sensitivity of the MSE at randomly generated subsamples ($n = 5, 10, 25, 50, 100, 200, 300, 400, 500$), re-generated 1000 times per sub-sample at 1.5m/s. Exponential curves describe this relationship well in all subjects. This relationship is observed here: combined mean of all 16 subjects (solid curve), individual walking speed trial mean of subjects with the highest (subject G, dotted curve) and lowest (subject M, dashed curve) overall MSE.

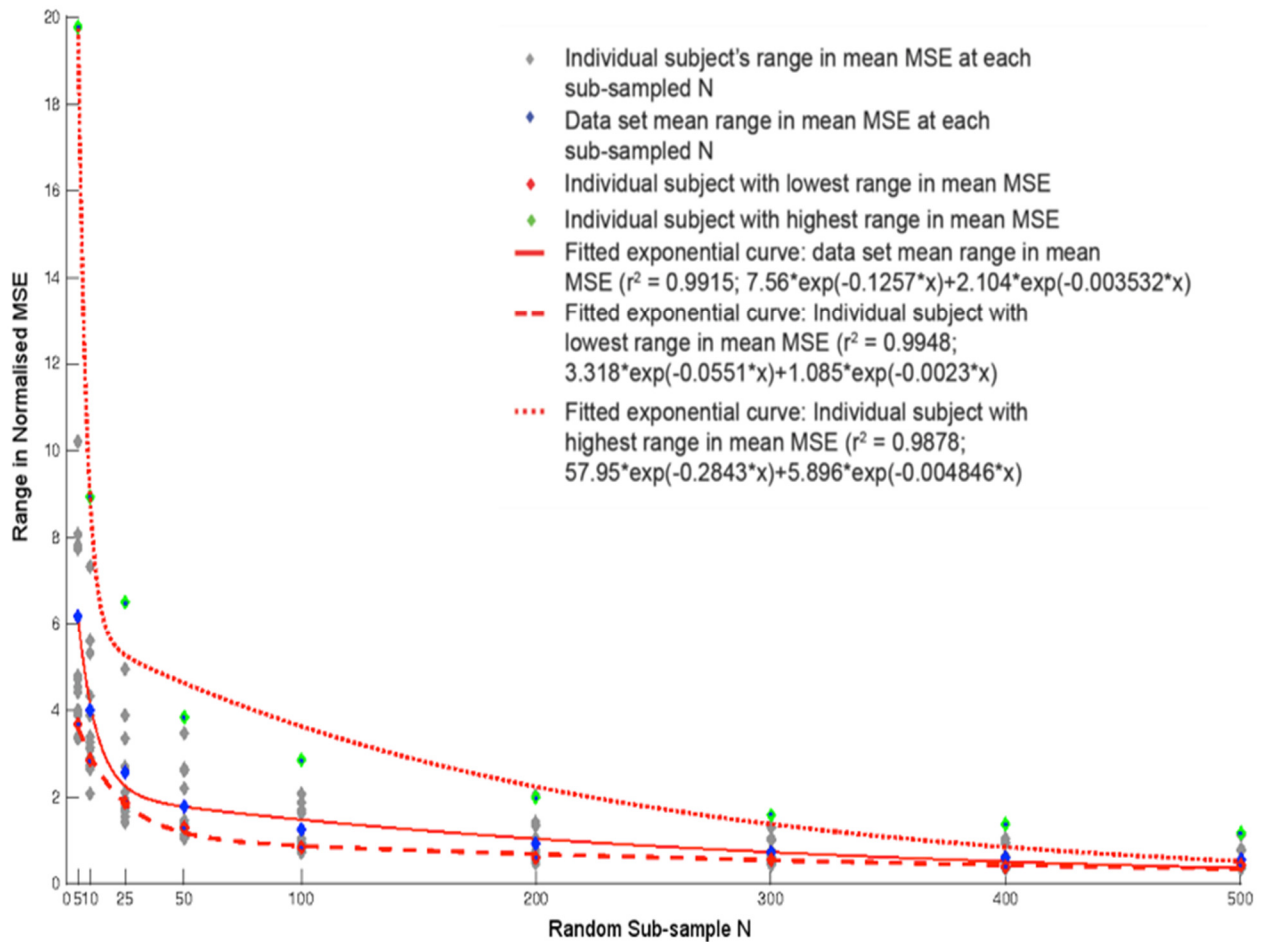


Figure S19. 3

The relationship between individual trial n and the sensitivity of the MSE at randomly generated subsamples ($n = 5, 10, 25, 50, 100, 200, 300, 400, 500$), re-generated 1000 times per sub-sample at 1.7m/s. Exponential curves describe this relationship well in all subjects. This relationship is observed here: combined mean of all 16 subjects (solid curve), individual walking speed trial mean of subjects with the highest (subject G, dotted curve) and lowest (subject M, dashed curve) overall MSE.

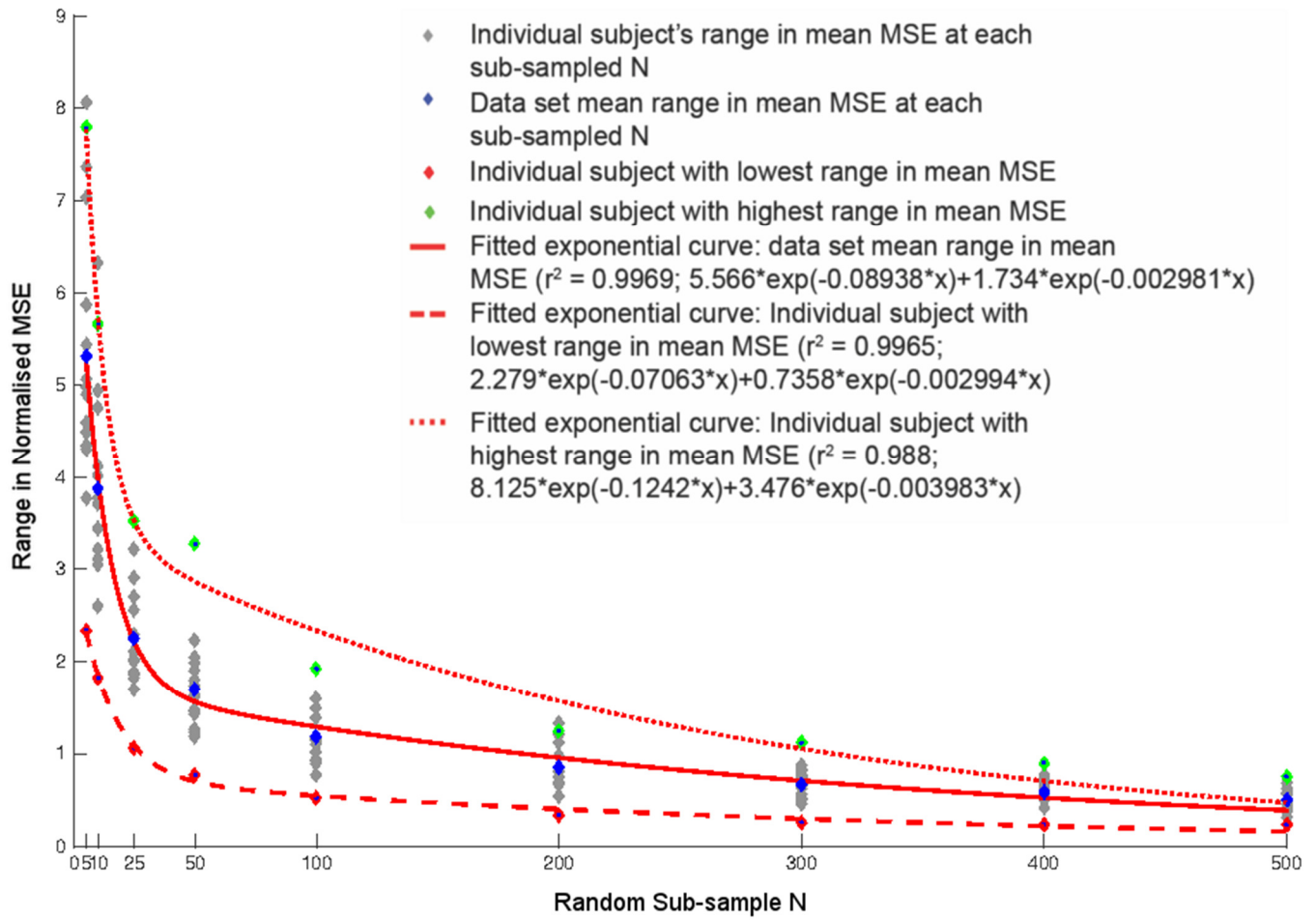


Figure S19. 4

The relationship between individual trial n and the sensitivity of the MSE at randomly generated subsamples ($n = 5, 10, 25, 50, 100, 200, 300, 400, 500$), re-generated 1000 times per sub-sample at 1.9m/s. Exponential curves describe this relationship well in all subjects. This relationship is observed here: combined mean of all 16 subjects (solid curve), individual walking speed trial mean of subjects with the highest (subject G, dotted curve) and lowest (subject M, dashed curve) overall MSE.

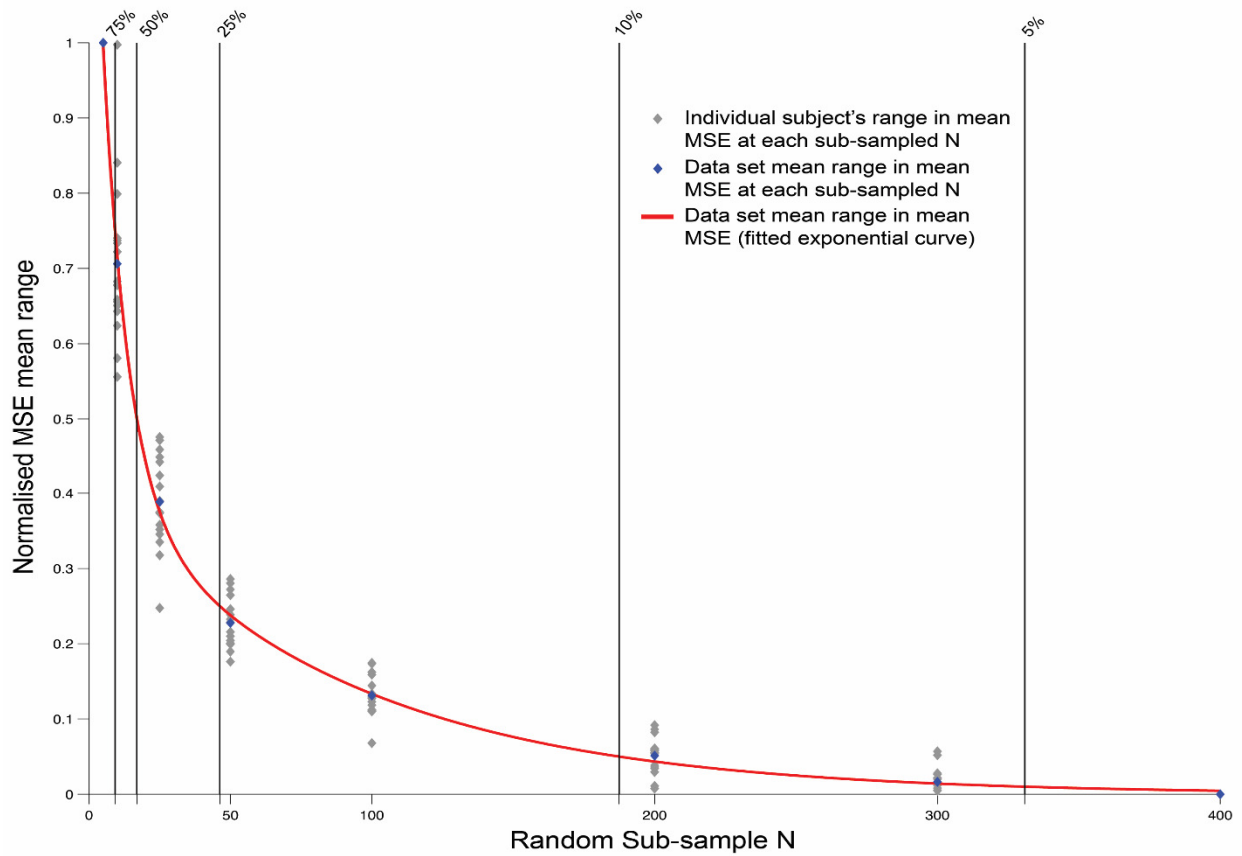


Figure S19. 5

The relationship between randomly generated subsample n (randomly generated 1000 times), and reports the n necessary to reach within 5%, 10%, 25%, 50% and 75% of the range in MSE at each subsample (vertical lines). The range in MSE is plotted as a percentage of the MSE value of the individual walking speed trial n , at 1.1m/s. When sample size is $n = >340$ pressure records, then the range in MSE (given by the 1000 randomly generated subsamples) is less than 5% of the individual walking speed trial MSE for each subject. The observed range in MSE at smaller individual trial $n = <25$ is only within 50% than the total individual trial MSE observed for each subject.

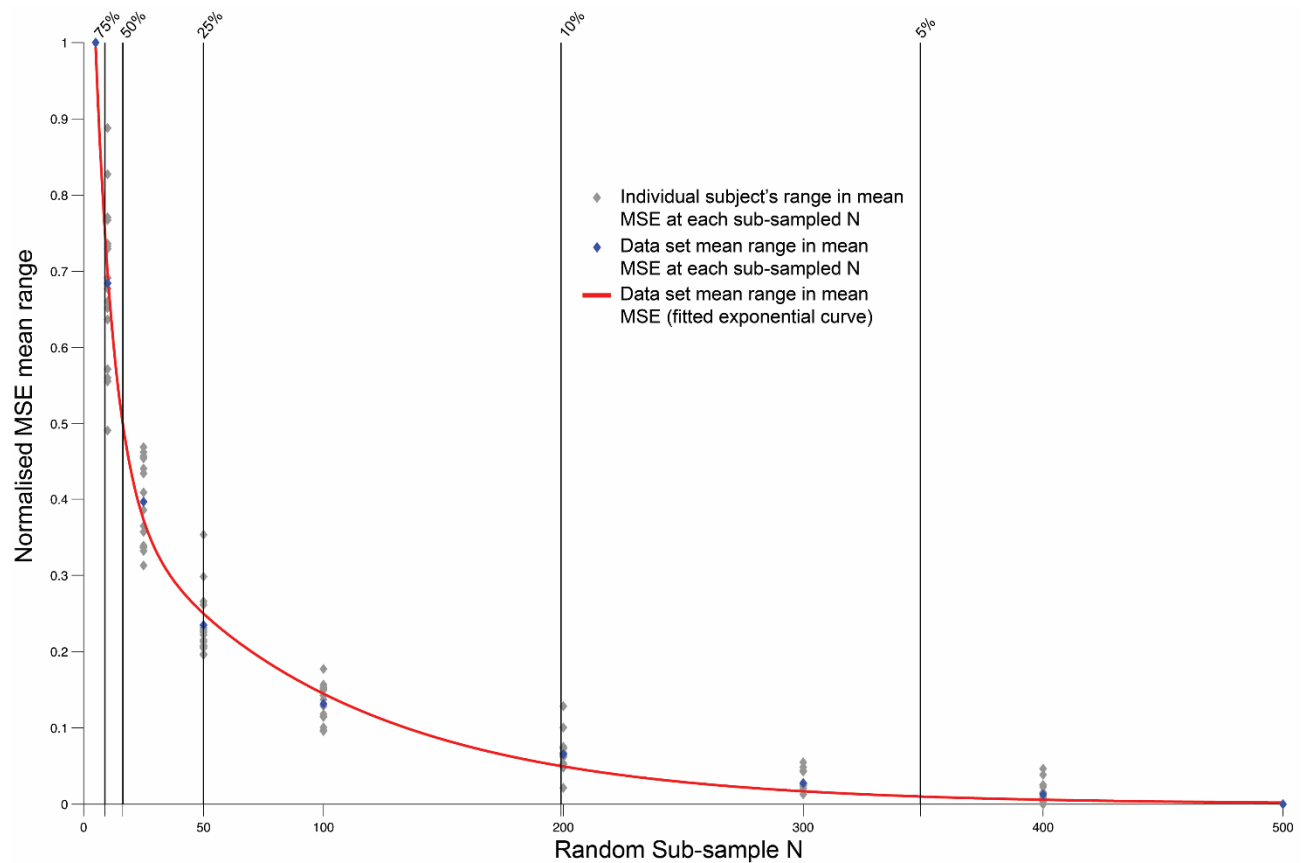


Figure S19. 6

The relationship between randomly generated subsample n (randomly generated 1000 times), and reports the n necessary to reach within 5%, 10%, 25%, 50% and 75% of the range in MSE at each subsample (vertical lines). The range in MSE is plotted as a percentage of the MSE value of the individual walking speed trial n , at 1.5m/s. When sample size is $n = >350$ pressure records, then the range in MSE (given by the 1000 randomly generated subsamples) is less than 5% of the individual walking speed trial MSE for each subject. The observed range in MSE at smaller individual trial $n = <25$ is only within 50% than the total individual trial MSE observed for each subject.

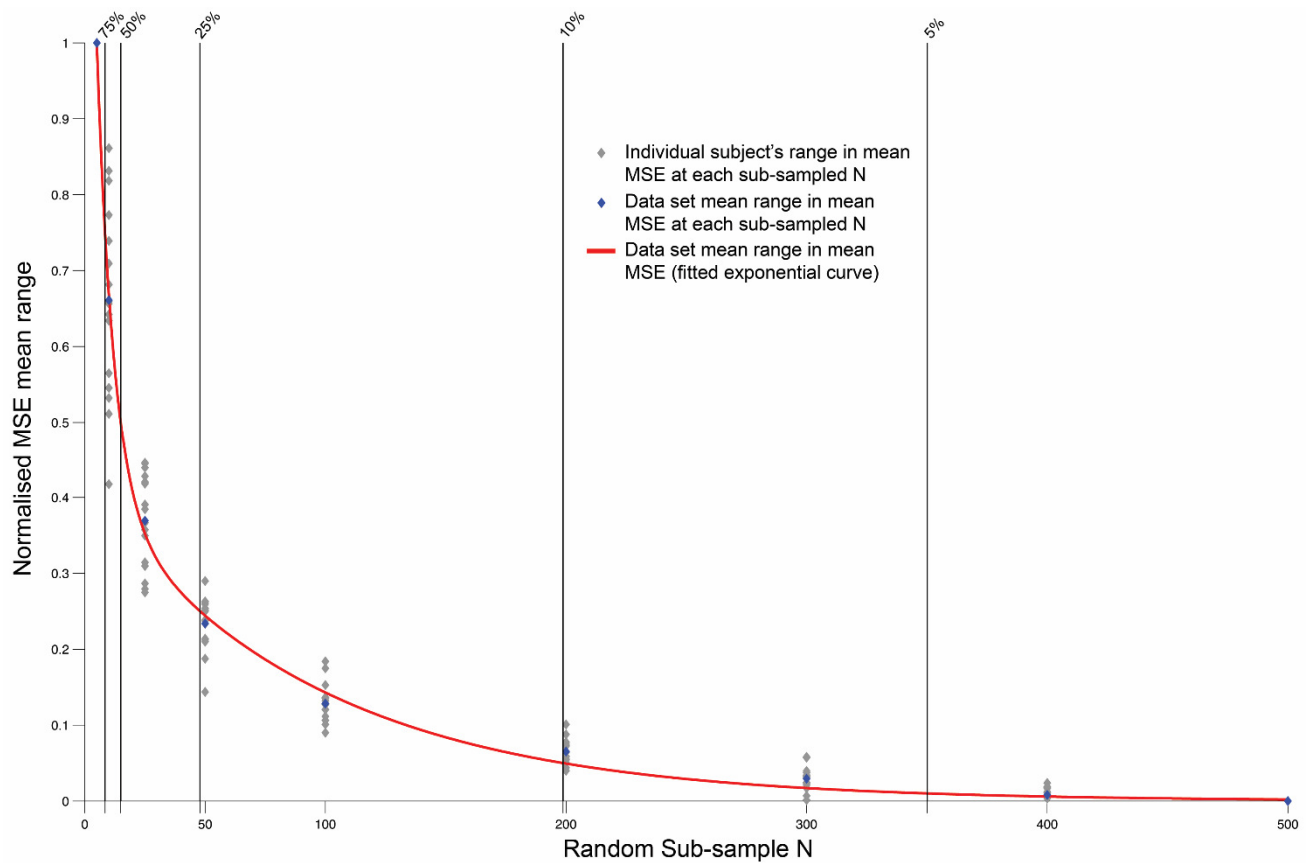


Figure S19. 7

The relationship between randomly generated subsample n (randomly generated 1000 times), and reports the n necessary to reach within 5%, 10%, 25%, 50% and 75% of the range in MSE at each subsample (vertical lines). The range in MSE is plotted as a percentage of the MSE value of the individual walking speed trial n , at 1.7ms. When sample size is $n = >350$ pressure records, then the range in MSE (given by the 1000 randomly generated subsamples) is less than 5% of the individual walking speed trial MSE for each subject. The observed range in MSE at smaller individual trial $n = <25$ is only within 50% than the total individual trial MSE observed for each subject.

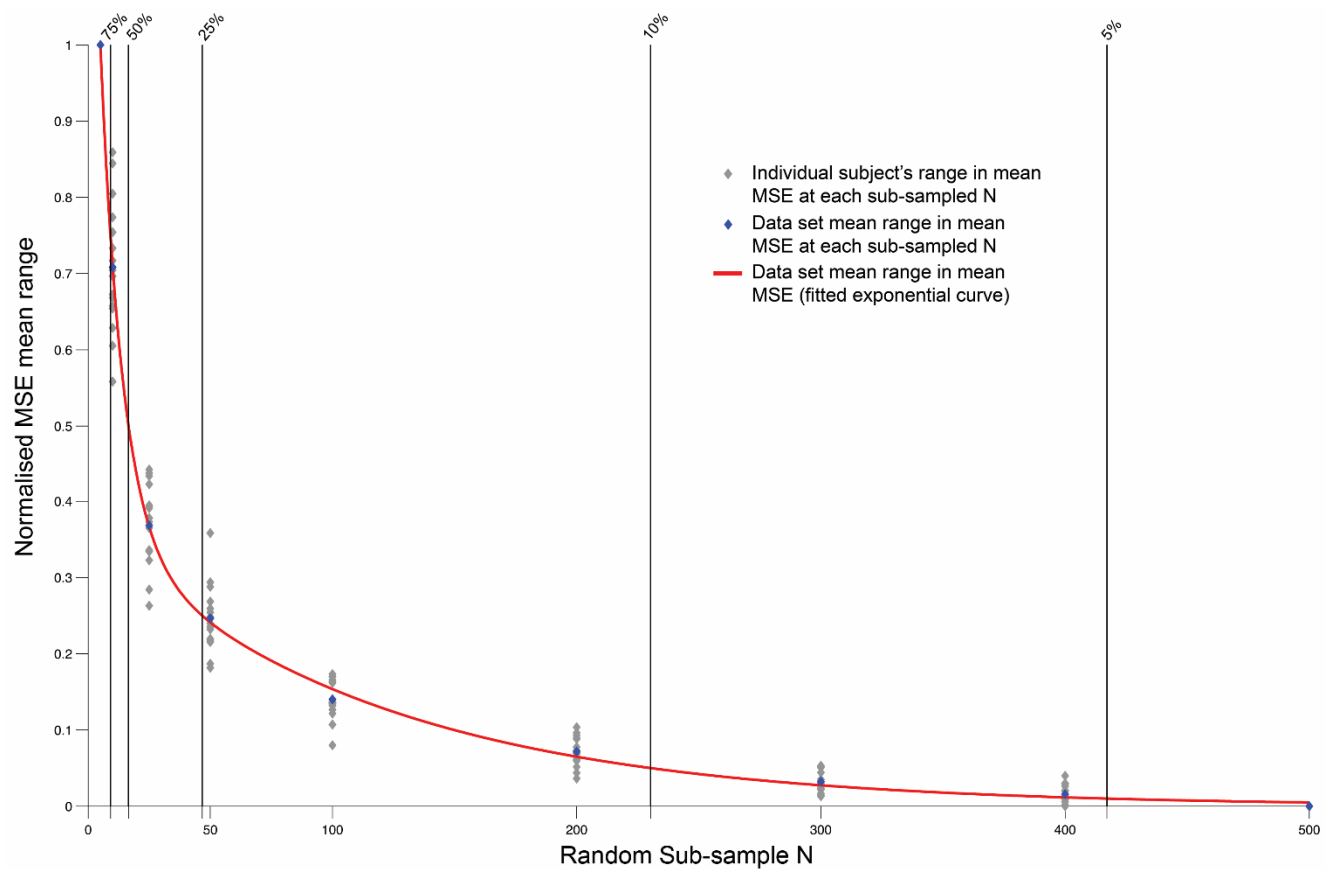


Figure S19. 8

The relationship between randomly generated subsample n (randomly generated 1000 times), and reports the n necessary to reach within 5%, 10%, 25%, 50% and 75% of the range in MSE at each subsample (vertical lines). The range in MSE is plotted as a percentage of the MSE value of the individual walking speed trial n , at 1.9ms. When sample size is $n = >420$ pressure records, then the range in MSE (given by the 1000 randomly generated subsamples) is less than 5% of the individual walking speed trial MSE for each subject. The observed range in MSE at smaller individual trial $n = <25$ is only within 50% than the total individual trial MSE observed for each subject.

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